

# Cretaceous trichotropid gastropods from the Pacific slope of North America: Possible pathways to calyptraeid morphology

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## ABSTRACT

Late Cretaceous gastropods belonging to genus *Lysis* Gabb, 1864, from the Pacific slope of North America, bridge the morphologic gap between turbiniform trichotropids and limpet-like calyptraeids. Development of the depressed and broadened inner lip/columella of *Lysis* resulted in a larger aperture that allowed more space for the foot to grasp a hard substrate. Pacific slope species of *Lysis* are represented by five species that collectively span an interval from late Coniacian to late Maastrichtian. They stem from two lineages of the trichotropine genus *Ariadnaria* Habe, 1961. The first lineage, which includes *Ariadnaria ainikta* new species of late Albion to Cenomanian age, *Ariadnaria stibara* new species of Cenomanian age, and *Ariadnaria obstricta* (White, 1889) of late Coniacian? and Santonian age, gave rise to the *Lysis duplicosta* group of neritiform to haliotiform, coarse-ribbed *Lysis*, including *Lysis mickeyi* new species (earliest *Lysis* in the world), *Lysis duplicosta* Gabb, 1864, *Lysis jalamaca* new species, and *Lysis lo-maensis* new species. The second lineage of *Ariadnaria* consists of the Turonian *Ariadnaria aldersoni* new species, which gave rise to the *Lysis suciensis* (Whiteaves, 1879) group. Morphologically, this group, which show crepiduliform and fine ribbed shells, appears likely to be a stem group from which Cenozoic *Crepidula*-like genera evolved. *Garzasia* new genus, which ranges from late Campanian or early Maastrichtian age to the mid Maastrichtian, evolved from the *Lysis duplicosta* group and includes *Garzasia intermedia* (Cooper, 1894) and *Garzasia diabla* new species. The very broad, depressed spiraling inner lip of *Garzasia* is suggestive of *Calyptraea* Lamarck, 1799. We propose placement of *Lysis* and *Garzasia* in *Lysinae* new subfamily of the Trichotropidae. In addition to their occurrence along the Pacific Slope of North America, *Lysis* or *Lysis*-like gastropods are known from middle Santonian to lower Campanian strata in South Africa, upper Campanian in the Congo, and Maastrichtian strata in Mozambique and Japan.

*Additional Keywords:* Trichotropidae, *Lysinae*, Calyptraeidae, evolution, paleogeographical occurrence

## INTRODUCTION

This study deals with the fossil record of the extinct genus *Lysis* Gabb, 1864, a small group of enigmatic gas-

tropods which has received little or no study regarding its ancestry, point of origin in terms of time and geographic locale, and evolutionary history. Specimens have been found in shallow-marine Cretaceous deposits from southern Vancouver Island and neighboring Gulf Islands, British Columbia, Canada to northern Baja California, Mexico (Figure 1) and, although *Lysis*-like gastropods have been reported at a few locales in the world, its familial placement has been uncertain. This study brings new information about all of these items.

Material for this study included type specimens, additional collections from their type localities, and specimens of Late Cretaceous age (Coniacian to Maastrichtian) from previously unreported-upon localities. Figure 1 provides an index to areas which yielded specimens used in this study.

During the study we discovered undescribed species of the trichotropine genus *Ariadnaria* Habe, 1961, which appear to have given rise to two groups of *Lysis*, a neritiform coarse-ribbed group and a crepiduliform fine-ribbed group. As will be discussed under "Evolutionary Implications," we propose that the neritiform group evolved into *Garzasia* new genus, which appears to be a precursor to calyptraeid genera.

A total of three genera (one of them new) and 11 species (seven of them new) make up this study. The taxa are: four species of *Ariadnaria* (three of them new), five species of *Lysis* (three of them new), and two species of *Garzasia* (one of them new). The ranges in time of all these species, as well as two recognizable groups of *Lysis*, are plotted on Figure 2. The *Lysis duplicosta* group consists of four species, spanning a total interval of late Coniacian to late Maastrichtian. This group was also the most geographically widespread, with specimens collected from British Columbia to Baja California. The *Lysis suciensis* group is known only from the Campanian to possibly early Maastrichtian, with specimens known from British Columbia to Baja California Sur. *Lysis* persisted for a total of approximately 18 million years in the study area.

The specimens studied here are mainly from fine-

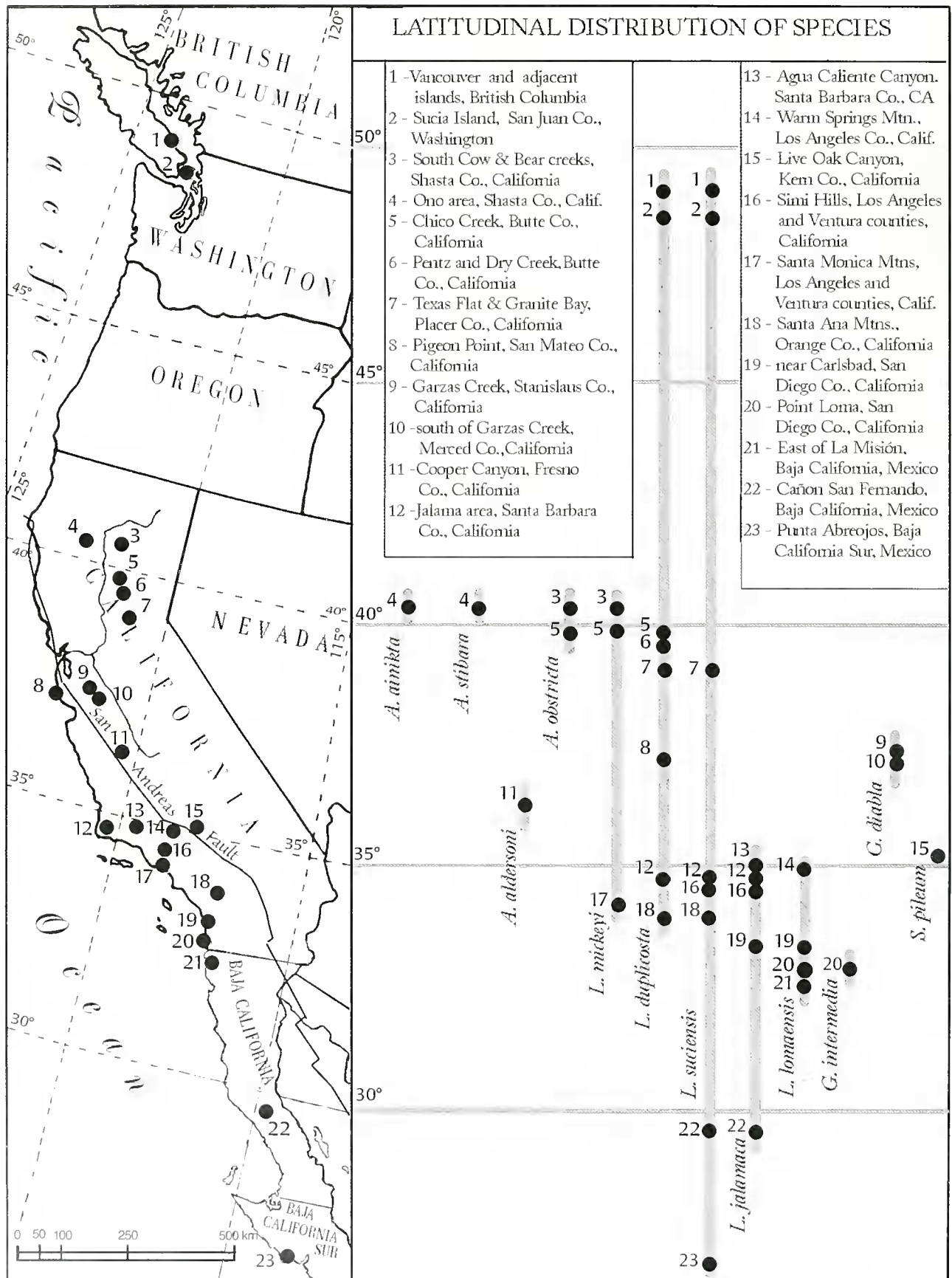
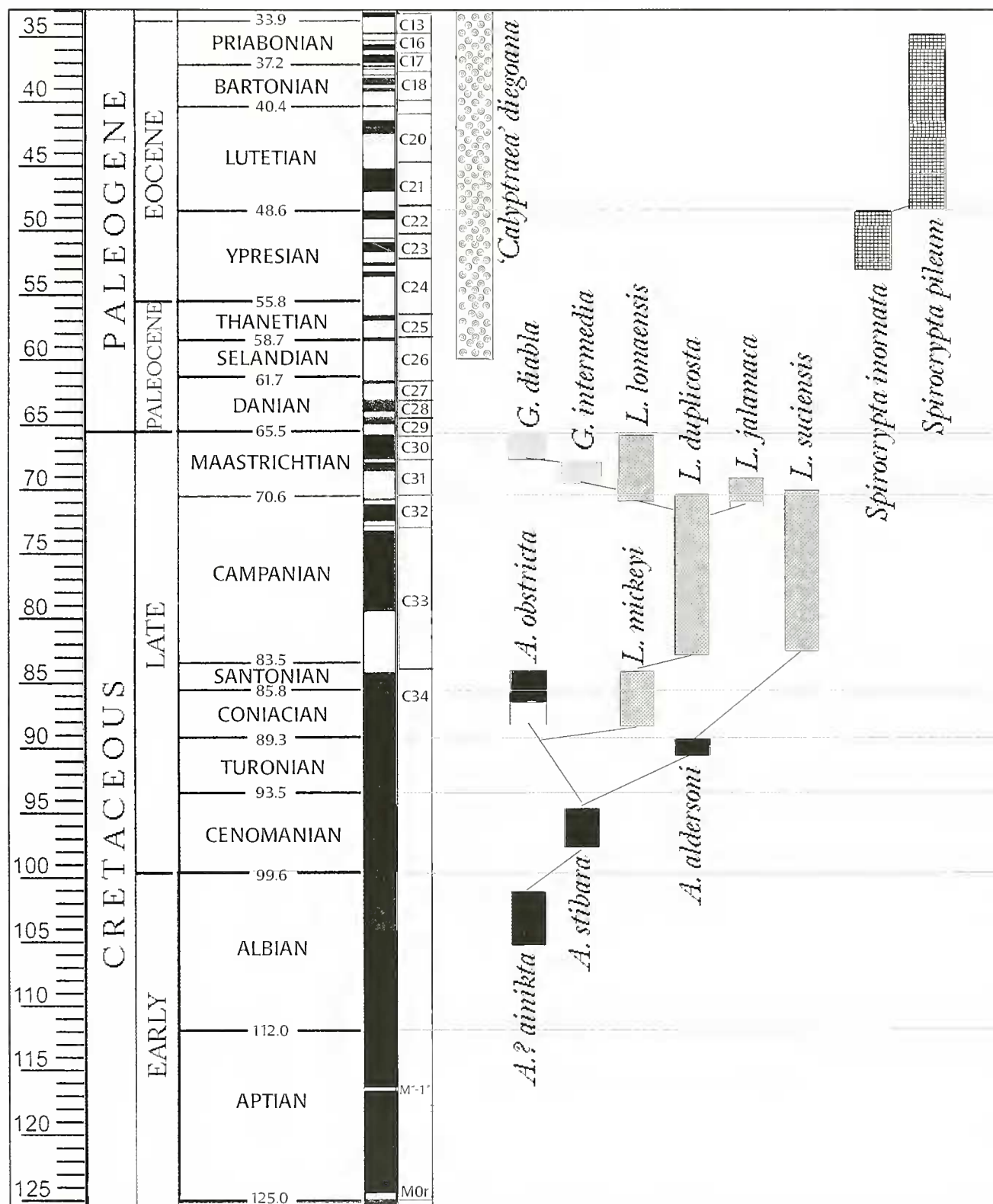


Figure 1. Index map of collecting localities.



**Figure 2.** Age ranges of species of *Ariadnaria*, *Lysis*, *Garzasia*, *Calyptraea*, and *Crepidula* discussed in text. Lines connecting the species indicate inferred descent based on morphologic similarity. *Lysis duplicosta* gave rise to two species one of which, *L. lomaensis*, produced proto-calyptraeid *Garzasia* and the other, *L. jalamaca*, is crepiduliform. An additional crepiduliform line was founded by *L. suciensis*. No known intermediate forms connect these Cretaceous calyptraeid and crepiduliform gastropods to Tertiary species. The earliest known Pacific Slope calyptraeid, '*C.* diegana' lacks the strong ribbing of *Garzasia*, but crepiduliform *Spirocrypta pileum* differs largely from *L. suciensis* in its small size. Time scale after Gradstein et al. (2004).



grained argillaceous sandstone or siltstone that constitute shelfal deposits that accumulated at depths near or just below wave base.

Specimens are low in number and almost always incomplete. Protoconchs are rarely preserved, the larval shell is in part missing, its shape partially represented by its inner cast in all available specimens. Apertures are usually missing their anteriormost area. Adhering matrix, commonly consisting of well-cemented sandstone usually plugs the aperture, thereby necessitating careful cleaning.

As will be discussed under "Evolutionary Implications," the shape of *Lysis*, with the exception of *L. mickleyi* new species, approaches that of *Crepidula*, resulting from flattening of the aperture, development of a broad shelf, and lateral coiling of the spire. The crepiduliform shape, as well as the *Calyptraea*-like shape of *Garzasia*, pose problems for terminology used for describing certain figures of specimens, as well as for describing certain shell dimensions. For some specimens, a full view of the aperture could only be depicted by having the the shell tipped out of the plane of its axis. The true height of these shells, therefore, is not shown; hence, the "vertical dimension" of the view is given instead, and perpendicular to it is the "horizontal dimension." In most cases, the abapertural view is in the plane of the shell axis; hence, the terms "height" and "diameter" apply.

Abbreviations used in the text are: ANSP: Academy of Natural Sciences of Philadelphia; CAS: California Academy of Sciences, San Francisco; CGS: Geological Survey of Canada, Ottawa; CIT: California Institute of Technology, Pasadena (collections now housed at LACMIP); CSMB: California State Mining Bureau (specimen at CAS); IGM: Instituto de Geología, Universidad Nacional Autónoma de México; LACMIP: Natural History Museum of Los Angeles County; SDNHM: San Diego Natural History Museum; UCLA: University of California, Los Angeles (collections now at LACMIP); UCMP: University of California, Berkeley, Museum of Paleontology; USGS: United States Geological Survey, Menlo Park (collections now housed at UCMP); USNM: National Museum of Natural History, Smithsonian Institution.

#### PALEOBIOGEOGRAPHIC DISTRIBUTION OF ARIADNARIA, LYSIS, AND GARZASIA

*Ariadnaria* ranges from late Albian to Recent with its earliest appearance in Pacific slope deposits of North America, where it is found in strata ranging from late Albian to Santonian age. From Japan, Kase (1990) figured, as *Trichotropis*?, a possible *Ariadnaria* species of earliest Maastrichtian age.

*Lysis* ranges from the late Coniacian to late Maastrichtian, and that is also its range for the Pacific slope of North America. The genus apparently originated in California, with five species known from the Pacific slope of North America. Four additional probable species of *Ly-*

*sis* are known elsewhere in the world. They are: *Lysis capensis* Rennie, 1930, from the middle Santonian to lower Campanian of South Africa (Kiel and Bandel, 2003); *Lysis congolensis* (Brébion, 1956) from upper Campanian of the Congo, Africa; *Lysis africana* (Cox, 1925) from the Maastrichtian (undifferentiated) of Mozambique; and *Lysis izumiensis* Kase, 1990, from the earliest Maastrichtian of Japan.

Rennie (1935) reported *Lysis caffra* Rennie, 1935, from the Upper Cretaceous near the eastern border of the Eastern Cape Province (Pondoland), southeast Africa, but its swollen naticiform shape with a very large, inflated body whorl and broad, non-depressed inner lip/columellar region, that appears to have a thin callus, are features not found in *Lysis*.

*Garzasia* ranges from late Campanian or early Maastrichtian to the mid Maastrichtian and is endemic to the Pacific slope of North America.

#### MODE OF LIFE OF LYSIS

*Lysis* has been found attached to a few specimens of large volutid gastropods. One specimen of *Longoconcha eumeka* Saul and Squires, 2008, from the Point Loma Formation near Carlsbad, California has two specimens of crepiduliform *Lysis jalamaca* new species on its shell, near the outer lip margin (Figure 34), as well as an attachment scar on the abapertural side of the shell. Specimens of *Lysis suciensis* from the Chatsworth Formation near Chatsworth, California, although not found in situ as are the younger Carlsbad specimens, have aperture shapes that could fit on the exterior of a specimen of *Volutoderma* Gabb, 1877. Indication of such an association is absent prior to middle Campanian. Whether the specimens of *Lysis* species were using dead shells as a substrate or had developed an association with living *Volutoderma* is undetermined.

Comparison to probable family members indicates that *Lysis* was a sedentary facultative ciliary feeder. Trichotropines, as well as calyptraeids, are ciliary feeders that live a sedentary life on hard substrates and are pro-trandrous hermaphrodites among whom brooding their young is common (Graham, 1954; Yonge, 1962). These mode-of-life characteristics have historically been used to classify trichotropines as being close to calyptraeids.

#### SYSTEMATIC PALEONTOLOGY

Superfamily Calyptraeioidea Lamarck, 1809

**Discussion:** The taxonomy of calyptraeoids, as with most gastropods, was traditionally based on shell morphology and later modified by increasing anatomical knowledge. The inclusion of patelliform Capulidae Fleming, 1822, turbiniform Trichotropidae, and coiled limpet-shaped Calyptraeidae in the superfamily Calyptraeioidea (e.g., Thiele, 1929; Wenz, 1940), has provided



calyptraeids a considerable morphological range and a somewhat complicated classification history (Bandel and Riedel, 1994). In addition to the above three families, Bandel and Riedel (1994), included Hipponicidae Troschel, 1861, in Calyptraeidea, but Collin (2003: 632) rejected hipponicids from a close relationship with calyptraeids. Ponder and Warén (1988) and Ponder (1998), equated family Capulidae with family Trichotropidae Gray, 1850, on anatomical grounds, reducing the included families to two. Capulids, as exemplified by *Capulus* Montfort, 1810, have limpet-shaped shells; trichotropids, as exemplified by *Trichotropis* Broderip and Sowerby, 1829, usually have coiled shells; and calyptraeids, as exemplified by *Calyptraea* Lamarck, 1799, *Crepidula* Lamarck, 1799, and *Crucibulum* Schumacher, 1817, have limpet-shaped shells with an internal shelf of variable shape.

In her analysis of calyptraeids, Collin (2003a, 2003b) utilized shell characters, anatomical characters, and molecular characters. Collin (2003a) argued that although the so-called echinospira larva of *Capulus* and of *Trichotropis* do not appear to be "true" echinospira, the thickened and elaborate larval shell of these two groups is clearly different from the simple larval shell of extant calyptraeids, and she (Collin, 2003a, 2003b, 2005) has continued to recognize the families Capulidae Fleming, 1822, Calyptraeidae, and Trichotropidae. Collin (2003a) mentioned that despite the detailed studies done on calyptraeids, their taxonomy remains contentious and uncertain. Because specimens studied here show no resemblance to capulids but do, in part, resemble trichotropids, and calyptraeids such as *Calyptraea* and *Crepidula*, we follow Collin in recognizing families Calyptraeidae and Trichotropidae.

Family Trichotropidae Gray, 1850

Subfamily Trichotropinae Gray, 1850

**Description:** Small to medium sized (usually 15 to 25 mm, but up to 40 mm in height), coiled, high-conic to broad, low-conic, or nearly cap-shaped; spiral sculpture usually better developed than collabral sculpture and represented by distinct cords and/or keels; umbilicus broadly open to slit-like or completely closed; aperture variable in shape, ranging from irregularly triangular and broadly oval to elongate-oval; some forms with more or less attenuated canal; operculum small, horny; radula taenioglossate; periostracum forming combs, bristles, spines usually in places of intersection of spiral and collabral sculpture (from Egorov and Alexeyev, 1998).

**Discussion:** Trichotropids provide the geologically oldest representatives of the three families Trichotropidae, Capulidae, and Calyptraeidae. We did not follow Ponder and Warén (1988), Ponder (1998), and Bouchet and Rocroi (2005) in placing Trichotropidae in Capulidae because trichotropids, such as the high spired *Ariadnaria* spp. discussed herein, differ distinctly from cap-shaped capulids. Collin (2003b) referred to trichotropids plus capulids as the closest outgroup to calyptraeids, sug-

gesting that she recognized these three as separate families. At present the geologic record finds trichotropids occurring earlier than capulids and also earlier than calyptraeids, and we suggest that based on species described herein, trichotropid-like gastropods gave rise to calyptraeids and that trichotropid specimens reported upon herein demonstrate a progressive development toward either a crepiduliform or a calyptraeiform shell.

*Atresius* Gabb, 1869, of Early Cretaceous (Valanginian to Hauterivian) age is the earliest trichotropine recognized by Wenz (1940), but its sole named species *A. liratus* Gabb, 1869, is a prominent constituent of chemosynthetic paleocommunities in northern California and probably not a trichotropid. *Lirpsa* Stephenson, 1952, of Cenomanian age from the Woodbine Formation of Texas may be the earliest previously known trichotropine. The earliest reported cap-shaped capulid is *Capulus verus* (Böhm, 1885) of Late Cretaceous (early Campanian) age from Aachen, Germany.

Genus *Ariadnaria* Habe, 1961

[= *Ariadna* Fischer, 1864; non Audouin, 1826].

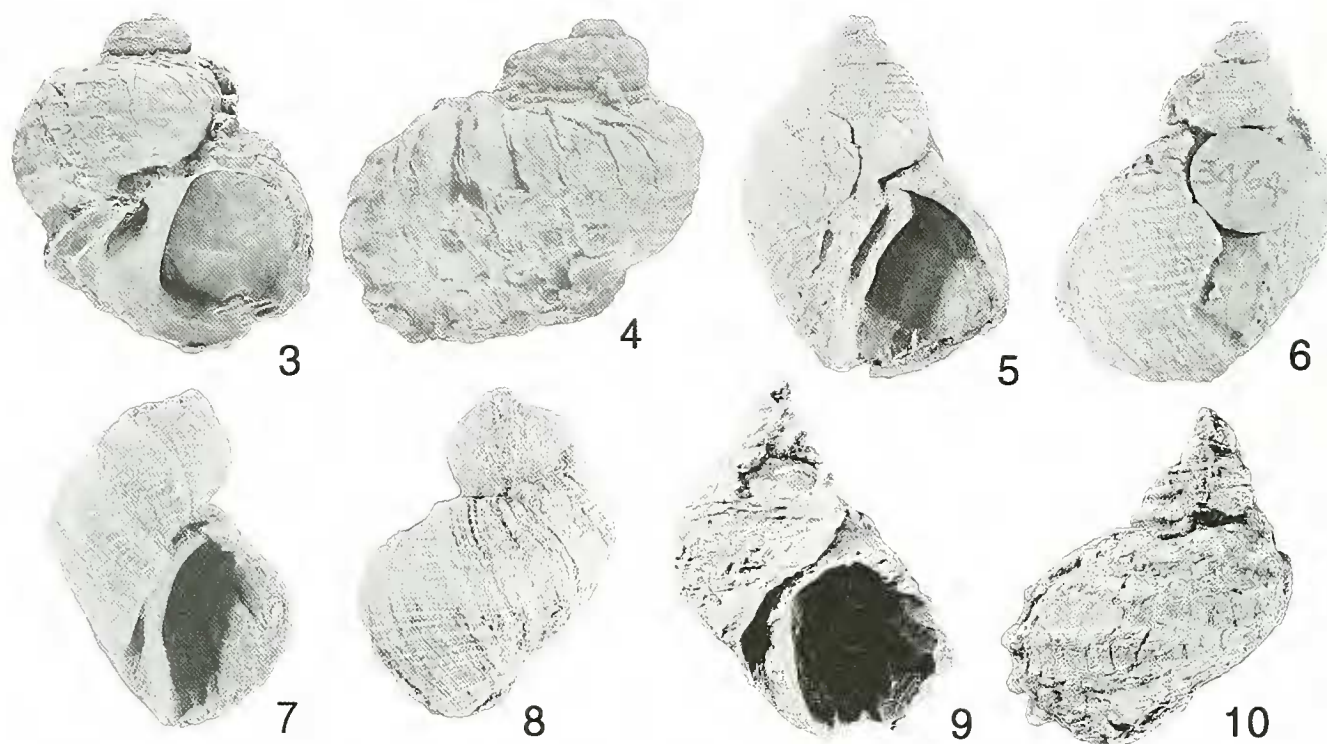
**Type Species:** *Trichotropis borealis* Broderip and Sowerby, 1829, by monotypy; boreal Arctic circumpolar (Egorov and Alexeyev, 1998) and cool temperate seas: northern North Atlantic south to Northumbria and all Scottish coasts (Fretter and Graham, 1962) and Massachusetts Bay (Emerson and Jacobson, 1976); the Bering Sea and north Pacific south to British Columbia (LACM collection, Forrester Island).

**Description:** Shell turbiniform (oval-conic) with raised spire; spiral sculpture well developed and consisting of raised cords separated by interspaces of variable width; collabral sculpture consisting of raised growth lines; aperture wide; inner lip slightly concave; canal short and straight; umbilicus slit-like; operculum thin; periostracum forming long, closely spaced bristles on spiral ribs.

**Discussion:** No prior records of *Ariadnaria* as a fossil were found by us. *Ariadnaria* differs from *Trichotropis* Broderip and Sowerby, 1829, by having an umbilicus. *Turbinopsis* Conrad, 1860, a turbiniform trichotropid of late Campanian or early Maastrichtian age from Mississippi, differs from *Ariadnaria* by having a wider umbilicus (profound according to Conrad, 1860), a last whorl that is more inflated and is tabulate, and having a very oblique fold near the basal margin of the columella.

*Ariadnaria ainikta* new species (Figures 3–4)

**Diagnosis:** Medium-size *Ariadnaria* with sturdy shell, rounded whorls, strong sculpture with nine spiral cords widely spaced; collabral sculpture thickly foliate; umbili-



**Figures 3–10.** *Ariadnaria* species. Specimens coated with ammonium chloride. **3–4.** *Ariadnaria ainikta* new species, holotype CAS 61794.00, CAS loc. 61791, height 20 mm, diameter 17 mm. **3.** Apertural view. **4.** Abapertural view. **5–6.** *Ariadnaria stibara* new species, holotype LACMIP 13371, LACMIP loc. 23464, height 19 mm, diameter 13.5 mm. **5.** Apertural view. **6.** Abapertural view. **7–8.** *Ariadnaria aldersoni*, holotype LACMIP 13372, LACMIP loc. 26370, height 12 mm, diameter 8.5 mm. **7.** Apertural view. **8.** Abapertural view. **9–10.** *Ariadnaria obstructa* (White, 1889), hypotype LACMIP 13373, LACMIP loc. 28717, height 21 mm, diameter 15 mm. **9.** Apertural view. **10.** Abapertural view.

cus elliptical; inner lip broad, expanded anterior and posterior to umbilicus.

**Description:** Shell medium (approximately 22 mm height), sturdy, turbiniform, spire moderately high, approximately 36% of total shell height; apical angle 110°; most of protoconch missing, remanent low and apparently smooth; teleoconch whorls three, whorls well rounded and enlarging very rapidly; suture appressed but appearing channeled; umbilicus open, deep, and elliptical; growth line prosocline; spiral sculpture consisting of regularly spaced and equally narrow cords; four cords on penultimate whorl; nine cords on last whorl, becoming stronger and more raised near umbilicus; spiral cords on last whorl widely spaced and occasionally with spiral thread in interspaces, especially anterior of periphery; collabral sculpture consisting of thickly foliate ridges coincident with growth checks, especially near outer lip; aperture D-shaped; inner lip broad, expanded anteriorly and posteriorly of umbilicus; abapertural edge of inner lip delineated by sharp ridge; basal lip broadened.

**Holotype:** CASC 61794.00, height 20 mm, diameter 17 mm, spire height 7.5 mm.

**Type Locality:** CASC loc. 61794 [=CASC loc. 1346-A].

**Distribution:** Basal Bald Hills Member of the Budden Canyon Formation, (area 4) Ono area, Shasta Co., California.

**Geologic Age:** Late Albian.

**Discussion:** Only the holotype is known. It evidently had a very foliate, thick shell. What remains is riddled with endobiont borings. Remnants of the protoconch are present, there is no clear evidence of an anterior sinus to the aperture, and the shell does not appear to have been nacreous.

The new species most resembles the trichotropid *Turbinopsis hilgardi* Conrad, 1860 (Conrad, 1860: 289, pl. 46, fig. 29; Sohl, 1960: 91, pl. 10, figs. 17, 18) from the upper Campanian/lower Maastrichtian Ripley Formation of Tippah Co., Mississippi, except *A. ainikta* has a smaller umbilicus and narrower cords with much wider interspaces. Additionally, the inner lip of *A. ainikta* is more expanded both anterior and posterior to the umbilicus.

*Ariadnaria ainikta* and *A. stibara* new species are similar in that there is no ridge separating the umbilicus from the inner lip. *Ariadnaria ainikta* differs from *A. stibara* by having a less elongate shell, wider penultimate whorl, stronger spiral cords with much wider interspaces, a shorter umbilicus that is oval rather than slit-like, foliate



collabral sculpture, and no parietal swelling on the inner lip. *Ariadnaria ainikta* differs from *A. aldersoni* new species by being larger, having much stronger spiral cords with much wider interspaces, a well rounded last whorl (not angulate), shorter umbilicus that is oval rather than slit-like, and no ridge separating the umbilicus from the inner lip. *Ariadnaria ainikta* differs from *A. obstricta* (White, 1889) by having a lower spire, wider penultimate whorl, round last whorl (not angulate) more spiral cords, foliate collabral sculpture, shorter umbilicus that is oval rather than slit-like, and no ridge separating the umbilicus from the inner lip. The strong spiral ribbing of *A. ainikta* resembles that of *A. obstricta*.

**Etymology:** *Ainiktos*, Greek, meaning: baffling, obscure, or enigmatic.

*Ariadnaria stibara* new species  
(Figures 5–6)

**Diagnosis:** A medium size sturdy *Ariadnaria* with rounded whorls, medium strong sculpture with many spiral cords moderately closely spaced; collabral sculpture very fine and lattice-like on spire whorls; umbilicus chink-like; inner lip with low parietal swelling.

**Description:** Shell medium small (height approximately 20 mm), sturdy, turbiniform, somewhat elongate, spire high and approximately 50% of total shell height; apical angle approximately 67°; protoconch not present; teleoconch whorls four, whorls well rounded and enlarging rapidly; last whorl tapering anteriorly; suture appressed, appearing channeled, and rapidly descending near aperture; umbilicus narrow, chink-like and present only adjacent to medial and posterior parts of inner lip; growth line prosocline, with several irregularly spaced growth checks near outer lip; spiral sculpture consisting of numerous fine subequal rounded cords: approximately ten closely spaced cords on penultimate whorl with interspaces of nearly equal width; approximately 18 cords on last whorl with interspaces slightly wider than cords; cords strongest, most widely spaced, and occasionally with spiral thread in interspaces on medial and anterior portions of last whorl; collabral sculpture consisting of thin, raised growth lines, forming nearly microscopic lattice-like pattern on spire whorls; aperture D-shaped, moderately large, oblique, narrowed at posterior end by low parietal swelling; inner lip broad, somewhat excavated (concave) medially and flattened anteriorly; abapertural edge of inner lip delineated by low but distinct ridge; basal lip broadened.

**Holotype:** Holotype LACMIP 13371, height 19 mm (incomplete), diameter 13.5 mm, spire height 9 mm.

**Type Locality:** LACMIP loc. 23464 is also type locality of *Turritiles dilleri* Murphy and Rodda, 1960.

**Distribution:** Bald Hills Member (unit IV of Matsmoto, 1960) of the Budden Canyon Formation, (area 4) Ono area, Shasta Co., California.

**Geologic Age:** Middle Cenomanian.

**Discussion:** Only the holotype is known, and it lacks the protoconch and the anterior end of the teleoconch. Whether or not an anterior siphonal notch was present is unknown, but the shape of the last whorl suggests that at least a small one was present. The species is assigned to *Ariadnaria* based on shell shape, but it differs from typical *Ariadnaria* in its very sturdy shell, the fineness of its sculpture, and the presence of a parietal swelling at the posterior end of the aperture.

*Ariadnaria stibara* differs from *A. ainikta* by having a more elongate shell, narrower penultimate whorl, much weaker spiral cords with much narrower interspaces, longer and narrower umbilicus, parietal swelling on inner lip, and absence of foliate collabral sculpture. *Ariadnaria stibara* differs from *A. aldersoni* by larger size, less elongate shell, more rounded whorls that are not lax in their coiling, coarser spiral ribs, lattice-like very fine collabral sculpture on spire whorls, parietal swelling on inner lip, less delineated abapertural edge of inner lip, and no fasciole-like flange bounding the umbilicus. *Ariadnaria stibara* differs from *A. obstricta* by having rounded whorls, many more spiral ribs that are much weaker and much more closely spaced, and a less well demarked abapertural edge of the inner lip.

**Etymology:** Named for its sturdy shell, *stibaros*, Greek, meaning strong or sturdy.

*Ariadnaria aldersoni* new species  
(Figures 7–8)

**Diagnosis:** Small *Ariadnaria* with elongate shell and last whorl medially subangulate, coiling stretched axially, whorls bearing many very fine and closely spaced ribs, umbilicus chink-like, spiral sculpture very fine, abapertural edge of inner lip well delineated and raised, umbilicus bordered by fasciole-like flange.

**Description:** Shell small (approximately 13.5 mm height, estimated); elongately turbiniform, with medially subangulate whorls; upper spire missing; teleoconch whorls enlarging rapidly; suture apparently appressed on earlier whorls, becoming channeled on penultimate whorl, rapidly descending; umbilicus chink-like, bounded by strong rounded fasciole-like ridge; growth line prosocline, well marked with numerous growth welts on last whorl; spiral sculpture consisting of fine, well spaced ribs of unequal strength crossing irregular growth welts; interspaces between ribs wider than ribs; aperture D-shaped, narrowed posteriorly but not angled, with short, broad anterior sinus; outer lip thin, simple; inner lip moderately narrow, abapertural edge raised and well demarked.

**Holotype:** LACMIP 13372, height 12 mm (incomplete), diameter 8.5 mm.

**Type Locality:** LACMIP 26370.

**Distribution:** Panoche Formation, (area 11) Alcalde Hills, Fresno Co., California.



**Geologic Age:** Late Turonian.

**Discussion:** Only the holotype is known. It is incomplete, consisting only of the last two whorls, and its small size may indicate that it is not mature. The elongate shape is a distinctive characteristic of this species. *Ariadnaria aldersoni* apparently had a relatively high spire, and the coiling is lax and reminiscent of *Lirpsa* Stephenson, 1952. It somewhat resembles *Lirpsa teres* Stephenson, 1952, but the new species has a narrow, chink-like umbilicus.

*Ariadnaria aldersoni* is most similar to *A. stibara* and differs by being smaller, having a more elongate shell, angulated whorls that are lax in their coiling, much weaker spiral ribs, abapertural edge of inner lip better delineated, fasciole-like ridge bounding the umbilicus, absence of lattice-like very fine collabral sculpture on spire whorls, and absence of parietal swelling on inner lip. *Ariadnaria aldersoni* differs from *A. ainikta* by being smaller, having much weaker spiral cords with much narrower interspaces, angulate last whorl, longer umbilicus that is slit-like rather than oval, and having a ridge separating the umbilicus from the inner lip. *Ariadnaria aldersoni* differs from *A. obstricta* by being smaller and having fewer and much weaker spiral cords with much narrower interspaces.

In some respects *A. aldersoni* is similar to *Lysis suciensis*. Both have fine ribbing, a relatively high spire, rather lax coiling, and a somewhat slower increase of whorl diameter. Whereas the suture of *A. obstricta* and *Lysis mickeyi* is very close to or at the perimeter of the previous whorl, in *A. aldersoni* and *Lysis suciensis* the suture is usually abapical to the previous whorl's perimeter.

**Etymology:** The species is named for John M. Alderson who collected the holotype from Cooper Canyon.

*Ariadnaria obstricta* (White, 1889)

(Figures 9–10)

*Stomatia obstricta* White, 1889: 18–19, pl. 4, figs. 10–11.

**Diagnosis:** Medium size *Ariadnaria* with high spire and angulate last whorl, sculpture of a few widely spaced strong cords, umbilicus chink-like or covered.

**Description:** Shell medium size (approximately 21.4 mm height), elongate turbiniform; whorl profile rounded with slight angulation at third strong cord on last whorl; spire high and approximately 50% of total shell height; apical angle approximately 67°; protoconch missing; teleoconch whorls four, enlarging rapidly and last whorl tapering anteriorly; suture appressed, anterior to subangulate periphery; umbilicus chinklike or covered by inner lip expansion; bounded abaperturally by strong ridge; growth line prosocline; sculpture of three strong, widely spaced cords on spire, five or six on body whorl; interspaces commonly with mid thread; aperture large and ovate with abapertural edge raised and sharply demarcated; outer lip apparently simple; inner lip somewhat expanded and standing high along umbilical chink; basal lip barely drawn out into slight spout-like sinus.

**Holotype:** USNM 20124.

**Type Locality:** Little Cow Creek but additional specimens have not been found there. The species is abundant at some localities along South Cow Creek, Shasta Co., California.

**Hypotype:** LACMIP 13373, height 20 mm, diameter 15 mm from LACMIP loc. 28717.

**Distribution:** Redding Formation, Bear Creek Sandstone Member, especially (area 3) along South Cow Creek and Bear Creek, Shasta Co.; Chico Formation, Musty Buck Member, (area 5) Chico Creek, Butte Co., California.

**Geologic Age:** Late Coniacian? to Santonian.

**Discussion:** The above description is based on 16 specimens; all but one are from LACMIP loc. 28717. Most specimens are poorly preserved, and specimens with the shell surface preserved are difficult to find. The primary cords are strong and almost flange-like.

White's species is here assigned to *Ariadnaria* based on shell shape, sculpture, umbilicus, and presence of a small spout-like sinus in the aperture. This would be the earliest unquestioned occurrence of this genus that previously was known only from the Recent (Wenz, 1940).

In shape and probably sculpture (preservation makes comparison difficult) *A. obstricta* resembles illustrations of *Trichotropis*? sp. in Kase (1990: 568, figs. 2.26, 2.27). Kase's specimen was from the Izumi Group of Japan of early Maastrichtian age.

*Ariadnaria obstricta* is very similar to *Lysis mickeyi* new species, but *A. obstricta* has more regular spiral ribs, a slightly higher spire, the strong spiral delimiting an umbilical chink, and a free standing inner lip. *Ariadnaria obstricta* differs from *Ariadnaria ainikta* by having a higher spire, narrower penultimate whorl, angulate last whorl, fewer spiral cords, shorter umbilicus that is slit-like rather than oval, ridge separating the umbilicus from the inner lip, and an absence of foliate collabral sculpture. *Ariadnaria obstricta* differs from *A. aldersoni* by being larger, having fewer spiral cords that are much stronger and much more widely spaced, and lacking a fasciole-like ridge bounding the chink-like umbilicus. *Ariadnaria obstricta* differs from *A. stibara* by having angulate whorls, fewer spiral ribs that are much stronger and much more widely spaced, and a more demarcated abapertural edge of the inner lip.

Subfamily Lysinae new subfamily

**Description:** Small to moderately large (15 to 80 mm in height), low turbiniform to almost haliotiform, barely siphonate shells with spiral ribbing. Final whorl somewhat to greatly enlarged; spire very short; aperture large, nearly circular to elongate oval; columella and inner lip flattened, expanded, and depressed to form a shelf within the aperture; some with shelf that spirals into an "umbilicus."

**Discussion:** The subfamily Lysinae includes *Lysis*

Gabb, *Garzasia* new genus, and probably *Spirogaucus* Finlay and Marwick, 1937. These gastropods are intermediate in form between trichotropines and calyptraeids. If their characteristics were better known, some other species such as those discussed under Global Distribution of Cretaceous Lysiform Gastropods, probably could be included here, some as *Lysis* or *Garzasia* others in as yet undescribed genera.

Genus *Lysis* Gabb, 1864

*Tropidothais* Cox, 1925: 213–214.

**Type Species:** *Lysis duplicosta* Gabb, 1864, by monotypy (Stewart, 1927: 345); Campanian of Pacific slope of North America.

**Description:** Turbinate to crepiduliform gastropods with a rapidly expanding whorl diameter having the columella/inner lip flattened, expanded, and submerged to form a narrow to broad shelf or deck. Shell sculptured by spiral cords or smooth. Nonumbilicate. Aperture with very slight anterior siphonal notch.

**Discussion:** *Lysis* differs from *Trichotropis* and *Ariadhuaria* in having the inner lip completely appressed to the columella. Typical *Lysis* (i.e., the group of *L. duplicosta*) has a carinated whorl in the juvenile stage and a few moderately strong to strong spiral cords. The stronger spirals are typically scaly. Included in this group is *L. duplicosta* and the following new species: *Lysis mickeyi*, *L. jalamaca*, and *L. lomaensis*. The group of *Lysis suciensis* has a more rounded whorl profile and more subdued, finer spiral sculpture; included in it is *L. suciensis*.

Group of *Lysis duplicosta*

The genus *Lysis* was proposed by Gabb (1864) for a low-spined, turbiniform gastropod with a depressed inner lip. He had only immature specimens of a single species (i.e., the type species) and did not recognize their similarity to genus *Crepidula* Lamarck, 1799. He gave no indication of the familial affinities of *Lysis*, other than stating the general form is like genus *Stomatia* Helbling, 1779.

During the last 127 years, *Lysis* has been placed in at least 11 families scattered among “archaeogastropods” to the neogastropods. A review of this placement history is given here. Species that were eventually placed in *Lysis* were originally placed in *Stomatia* of the Stomatellidae Gray, 1840, by Whiteaves (1879, 1903) and White (1889). Stoliczka (1867–1868: 157–158) suggested that *Lysis* should be placed near *Separatista* Gray, 1847, in the Trichotropidae Gray, 1850, in the event that *Lysis* does not belong in either the Naticidae Guilding, 1834, or the Velutinidae Gray, 1840. Fischer (1885) placed *Lysis* in the Naticidae near *Eunaticina* Fischer, 1885. Tryon (1884: 112) did not hesitate to refer *Lysis* to the Muricidae Rafinesque, 1815 (as *Murexia*) [= Purpuradae Children, 1823], but on page 208 Tryon suggested a relationship to *Velutina* Fleming, 1821, of the Lamellaridae d’Orbigny, 1841. Cossmann (1903) wrote that *Lysis* could not be a muricid but must be placed near *Fossarus*

Philippi, 1841, presumably in the Fossaridae Adams, 1860, where Stewart, 1927, Rennie (1930), Wenz, 1940, and Anderson (1958) also put it. Cossmann (1925) considered *Lysis* to be a subgenus of *Micreschara* Cossmann (1891) in the family Vanikoroidae Gray, 1840. Dall in Eastman (1913) and Packard (1922) placed *Lysis* in the “Thaistiidae” (=Thaididae) Suter, 1909. Saul (1959) and Saul and Alderson (1981) placed *Lysis* in Calyptraeidae, and, in 1990, Saul included it in superfamily Calyptraeioidea. Kase (1990) discussed previous taxonomic treatments of *Lysis* and suggested that, based on its inner lip shelf, the genus should be placed within the Calyptraeidae Lamarck, 1799. Bandel and Riedel (1994) and Kiel and Bandel (2003) supported this placement. Cox (1925) named and described genus *Tropidothais* Cox, 1925, which is a junior synonym of *Lysis*. He based *Tropidothais* on *T. africana* Cox, 1925, from the Maastrichtian of Mozambique [formerly Portuguese East Africa] and tentatively placed his genus in the Thaididae Jousseaume, 1888. Upon realizing its similarity to *Lysis*, Cox (in Rennie, 1935) synonymized the two genera and placed *Lysis* in the Stomatellidae. In this present paper, we place *Lysis* in the family Trichotropidae, subfamily Lysinae because *Lysis* appears to have evolved from trichotropids by expanding the columella/inner lip area (width and length) to form an interior shelf suggestive of the calyptraeid *Crepidula*.

*Lysis mickeyi* new species.

(Figures 11–16)

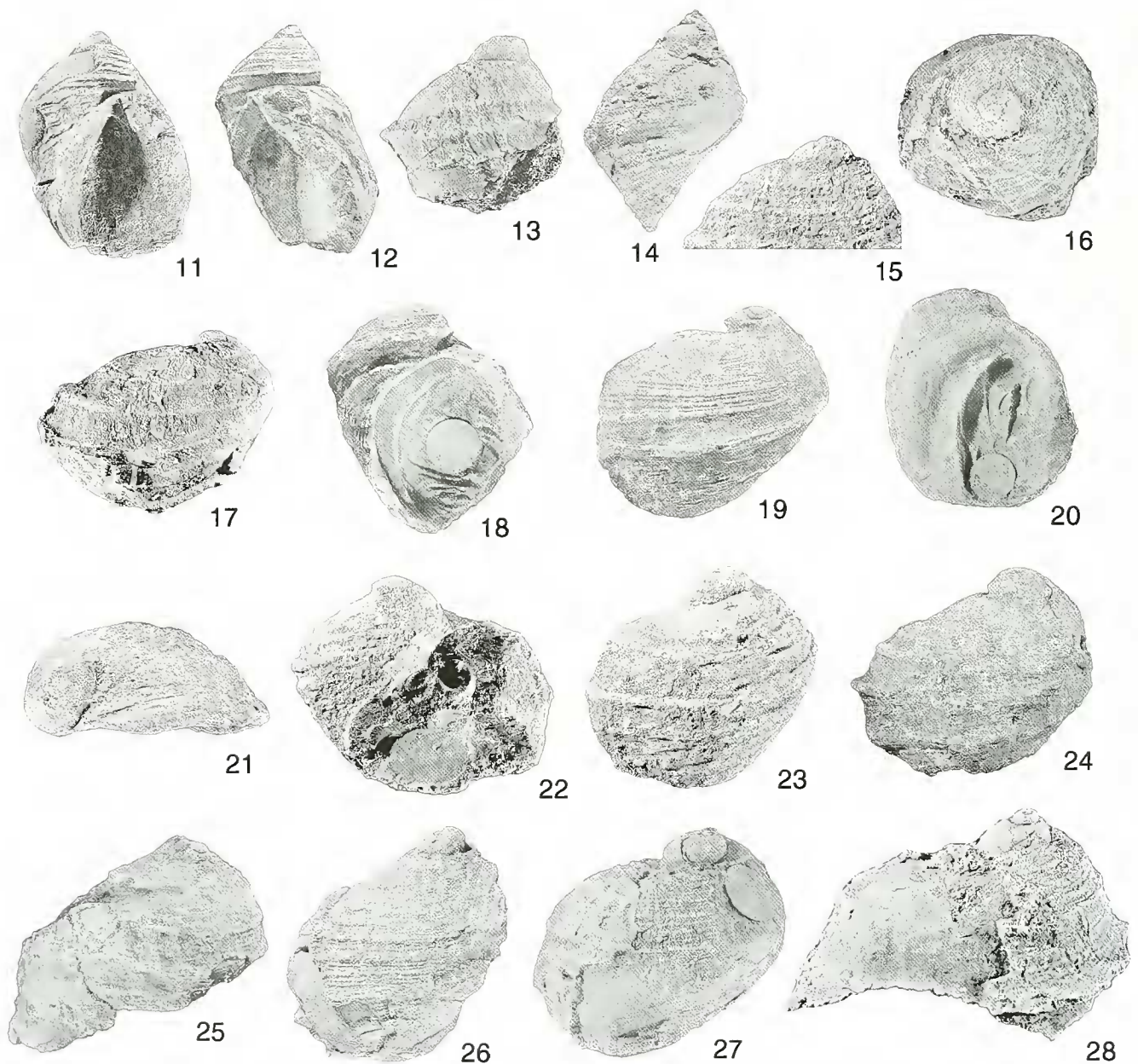
**Diagnosis:** A relatively high spired *Lysis* with eight or nine strong cords on last whorl; shelf moderately broad, somewhat depressed, and shallowly concave.

**Description:** Shell medium small (height approximately 20 mm), turbiniform; whorl profile overall rounded with medial angulation on last whorl; spire moderately low and approximately 30% of total shell height; apical angle approximately 90°; protoconch 1.5 whorls, low and smooth; teleoconch whorls 3.5, moderately expanding and last whorl tapering anteriorly; suture abutting and becoming laxly channeled on later whorls; sculpture of strongly raised cords, either moderately closely spaced or widely spaced; penultimate whorl with two to six and last whorl with eight or nine strong spirals, with variable number (two to five) of finer spirals in interspaces; both cords and interspaces crossed by fine collateral ribs, producing beaded appearance; angulation moderately strong on last whorl, coincident with strongest spiral cord; spiral cord anterior to angulation nearly same strength, thereby producing bicarinate appearance to medial part of last whorl; aperture large, oblique, barely notched anteriorly; outer lip simple; shelf moderately broad, somewhat depressed, and shallowly concave.

**Holotype:** LACMIP 13374, height 13 mm, diameter 9.5 mm, spire height 5 mm.

**Paratypes:** LACMIP 13375 from LACMIP loc. 23617 and 13376 and 13377 from LACMIP loc. 10757.





**Figures 11–28.** *Lysis* species. 11–16. *Lysis mickeyi* new species. 11–12. Paratype LACMHP 13375, LACMHP loc. 23617, height 21 mm, diameter 16 mm. 11. Apertural view. 12. Right-lateral view. 13. Paratype LACMHP 13376, LACMHP loc. 10757, left-lateral view, height 9 mm, diameter 11 mm. 14. Holotype LACMHP 13374, LACMHP loc. 10757, abapertural view, height 13 mm, diameter 9.5 mm. 15–16. Paratype LACMHP 13377, LACMHP loc. 10757, height 5 mm, diameter 9 mm. 15. Left-lateral view. 16. Apical view. 17–28. *Lysis duplicosta* Gablb, 1864. 17. Plasto-lectotype of *Stomatia suciensis carinifera* Whiteaves, 1879, CGS 5772, height 10 mm, diameter 19.5 mm. 18–19. Hypotype LACMHP 13378, LACMHP loc. 24128. 18. Apertural view, vertical dimension 27 mm, horizontal dimension 21 mm. 19. Abapertural view, height 22 mm, diameter 26.5 mm. 20–21. Hypotype LACMHP 13379, LACMHP loc. 24340. 20. Apertural view, vertical dimension 28 mm, horizontal dimension 25 mm. 21. Lateral view, vertical dimension 13 mm, horizontal diameter 29.5 mm. 22–23. Hypotype LACMHP 13380, LACMHP loc. 24340, height 19 mm, diameter 18 mm. 22. Apertural view. 23. Abapertural view. 24. Hypotype LACMHP 13381, LACMHP loc. 24340, abapertural view, vertical dimension 28 mm, diameter 37.5 mm. 25. Hypotype LACMHP 13382, LACMHP loc. 24349, abapertural view, height 17 mm, diameter 22 mm. 26. Hypotype LACMHP 13383, LACMHP loc. 10095, crushed specimen, abapertural view, height 24 mm, diameter 22.5 mm. 27. Hypotype LACMHP 13384, LACMHP loc. 26951, abapertural view, height 21 mm, diameter 25 mm. 28. Hypotype LACMHP 13385, LACMHP loc. 24340, abapertural view, height 7.5 mm, diameter 12 mm.



**Type Locality:** LACMIP loc. 10757.

**Distribution:** Redding Formation, Bear Creek Sandstone Member of Haggart (area 3) on Bear Creek, Shasta Co.; Chico Formation, top of Ponderosa Way Member and Musty Buck Member (200 m to 650 m above the base of the section) (area 5) on Chico Creek, Butte Co.; basal Tuna Canyon Formation (area 17) at head of Garapito Creek, Santa Monica Mountains, Los Angeles Co., California.

**Geologic Age:** Early Coniacian to Santonian.

**Discussion:** The above description is based on 80 specimens; most of these are from LACMIP locs. 10846 and 23617. Most specimens are internal molds. Many show endobiont boreholes, especially on the spire whorls. Two specimens show the protoconch. The oldest specimen is from LACMIP loc. 26967 in the Santa Monica Mountains.

*Lysis mickeyi* resembles *Lysis suciensis* (Whiteaves, 1879) in height of spire but is closer to *L. duplicosta* in sculpture. *Lysis mickeyi* differs from *L. duplicosta* in having a higher spire, less expanding last whorl, much less expanded shelf, more oval aperture, and thinner spiral cords. *Lysis mickeyi* greatly resembles *Trichotropis obstricta* (White, 1889), but on *L. mickeyi* the spiral ribs are less regular, and its spire is slightly lower. In addition, *L. mickeyi* lacks an umbilical chink and a free-standing inner lip.

*Lysis mickeyi* is the earliest known *Lysis* from anywhere in the world.

**Etymology:** Named for Mickey of Mickey's House on Chico Creek near the locality, LACMIP 23617, from which the species was first recognized.

*Lysis duplicosta* Gabb, 1864  
(Figures 17–28)

*Lysis duplicosta* Gabb, 1864: 138, pl. 21, fig. 9Sa–9Sc; Tryon, 1853: 112, pl. 44, fig. 25–26; Cossmann, 1903: 70; Stewart, 1927: 345–346, pl. 21, figs. 7, 7a; Anderson, 1955: 169.

*Stomatia suciensis* variety *carinifera* Whiteaves, 1879: 128–129, pl. 16, fig. 5.

*Lysis oppansus* White, 1889: 17, pl. 4, figs. 14–15; Anderson, 1955: 169.

*Lysis suciensis* var. *carinifera* (Whiteaves).—Whiteaves, 1903: 367, pl. 45, fig. 4.

*Microschara* (*Lysis*) *duplicosta* (Gabb).—Cossmann, 1925: 173, pl. 9, figs. 6, 21.

*Lysis duplicostata* Gabb.—Wenz, 1940: 580, fig. 2587 (reprint of Stewart, 1927); Elder and Saul, 1993: pl. 2, figs. 14–15.

*Lysis carinifera* (Whiteaves).—Anderson, 1955: 170.

? *Lysis duplicosta carinifera* (Whiteaves).—Dailey and Pope-noe, 1966: 6.

Not *Lysis duplicosta* Gabb.—Saul and Alderson, 1981: 35–36, pl. 3, figs. 3–4 [= *Lysis suciensis* (Whiteaves) *vide* Saul, 1990].

**Diagnosis:** Variably sculptured *Lysis*, with many fine cordlets or with six to eight strong cords, including prominent (often flange-like) carina on periphery; columella and inner lip depressed and expanded to form

crenate shelf, occupying at least one third of aperture in larger specimens.

**Description:** Shell medium size (height up to approximately 26 mm), neritiform to crepiduliform; spire moderately low, approximately 20% of total shell height; protoconch 1.5 whorls, low and smooth; teleoconch approximately two whorls, overall rounded, enlarging very rapidly, and medially carinate; sculpture consisting of spiral ribs, generally six to eight prominent ones, but highly variable in number, spacing, and strength; periphery always demarked by very strong (occasionally flange-like) carina, located anteriorly of medial position on spire whorl and located medially on last whorl; remainder of whorls covered by spiral sculpture, ranging from numerous closely spaced fine cordlets to several widely spaced moderately strong (can alternate in strength) cords, with interspaces smooth or bearing many cordlets or threads; cords just anterior and, to a lesser degree, just posterior of medial carina on last whorl commonly approaching strength of medial carina, thereby imparting either a bicarinate or tricarinate appearance to whorl profile; aperture circular with a scarcely discernable anterior canal notch; abapertural edge of aperture sharply demarked by raised edge; inner lip and columella flattened, and expanded to form shelf; shelf moderately wide (occupying at least one third of aperture in larger specimens), submerged within the aperture, wrapping far past suture and attached to inside of outer lip; medial part of outer lip digitate.

**Lectotype:** Of *Lysis duplicosta* UCMP 11975, height 10 mm, diameter 19.5 mm. Gabb (1864) did not indicate a holotype. Merriam (1895) recognized UCMP 11975 as the figured specimen. Stewart's (1927) statement that this is the type specimen is taken as designation of lectotype.

**Paralectotype:** Of *Lysis duplicosta* ANSP 4242.

**Syntypes:** *Stomatia suciensis* variety *carinifera* Whiteaves, 1879, CGS 5772, a–d (Bolton, 1965). Whiteaves (1903: pl. 16, fig. 5) figured one of the five syntypes CGS 5772.

**Holotype:** Of *Lysis oppansus* White, 1889, USNM 20115.

**Hypotypes:** Of *Stomatia suciensis carinifera*, CGS 5939 (Whiteaves, 1903); Of *Lysis duplicosta* LACMIP 13378–13385; USNM 468585, 468586.

**Type Locality:** Of *Lysis duplicosta*, Texas Flat, near Rock Corral, from a mine shaft at a depth of 12 m [40 ft.], near the Placer-Sacramento Co. line, Placer Co., northern California; Of *Stomatia suciensis carinifera*, Sucia Island, San Juan Co., Washington. Of *Lysis oppansus*, Pentz Ranch, Butte Co., northern California.

**Distribution:** Cedar District Formation, Nanaimo Basin, (area 1) Vancouver Island area, southern British Columbia and (area 2) Sucia Island, San Juan Co., Washington; Chico Formation, Ten Mile Member on (area 3)

Chico Creek and Musty Buck Member along (area 6) Dry Creek, near Pentz, Butte Co., California; Chico Formation, (area 7) Granite Bay and Texas Flat, Placer Co., California; Pigeon Point Formation, southern sequence, (area 8) north of Pigeon Point, San Mateo Co., California; Jalama Formation, (area 12) western Santa Ynez Mountains, Santa Barbara Co., California; Ladd Formation, uppermost Holz Shale Member and Williams Formation, Schulz Member, (area 18) Santa Ana Mountains, Orange Co., California.

**Geologic Age:** Campanian.

**Discussion:** The above description is based on 101 specimens; most of these are from the Pentz area (LACMIP loc. 24340). At any locality, most of the specimens are internal molds. Some show endobiont boreholes. One specimen, LACMIP 13385 (Figure 28), shows the shape of the protoconch.

The holotype of *Lysis duplicosta* is a juvenile and had not yet developed the wider deck of an adult. The largest specimens of this species thus far found are from the Musty Buck Member of the Chico Formation at LACMIP loc. 24340 near Pentz (area 6). The specimens are from a matrix-supported pebble conglomerate richly fossiliferous in places. The fauna, which includes scraps of cypraeids, suggests warm, shallow water. *Lysis duplicosta* is very rare in the coeval Ten Mile Member on Chico Creek (area 5) which probably represents deeper water than at LACMIP 24340, and the specimen from LACMIP loc. 23639 on Chico Creek may have been transported downslope.

The strength of the cords, especially of the strongest one, varies greatly between individuals. Gabb's specific name refers to a doubled appearance of each major cord, but Gabb's (1864) sharp, deep channel along the strong ribs results from the wearing or breaking off of the scales on the ribs.

Dailey and Popenoe (1966: fig. 3) listed *Lysis duplicosta carinifera* from the Jalama Formation at LACMIP loc. 24128. This somewhat distorted specimen (Figures 18, 19) has some stronger ribs as in *L. duplicosta*, but may represent a strong ribbed variant of *L. jalamaca*. If *L. duplicosta*, it is the geologically youngest specimen of this species.

Rennie (1930: 1935) described two species of *Lysis* from the Umzamba Formation of the Eastern Cape Province (formerly Pondoland), South Africa, one of which *Lysis capensis* Rennie, 1930, is very similar to *L.*

*duplicosta*. According to Klinger and Kennedy (1980), the lower Umzamba Formation at its type locality is latest Santonian or earliest Campanian in age and, therefore, similar in age to the Chico Formation near Pentz, Butte Co., California, where *L. duplicosta* is common. Rennie apparently had only two specimens of *L. capensis* which he said had six stout, sharp, spiral ribs. His holotype is small, similar in size to the holotype of *L. duplicosta*, and both apparently have a relatively narrower deck than is found in large specimens of *L. duplicosta*.

Kase's (1990) report of *L. duplicosta* in the Chatsworth Formation is based on a misidentification of *L. suciensis* in Saul and Alderson (1981).

*Lysis jalamaca* new species

(Figures 29–36)

*Lysis duplicosta* Gabb.—Dailey and Popenoe, 1966: 6. Not *Lysis duplicosta* Gabb, 1864.

**Diagnosis:** A *Lysis* with sculpture of fine spiral cordlets of alternating strength and within the aperture the shelf wrapping considerably past suture.

**Description:** Shell medium size (height up to 26 mm), crepiduliform, with rapidly expanding whorls; spire low, and approximately 30% of total shell height; protoconch 1.5 whorls, low and smooth; teleoconch approximately two whorls, well rounded; whorls flattened adjacent to suture; periphery near mid-whorl height; suture abutting just below periphery; growth line prosocline, occasionally forming collabral wrinkles; sculpture consisting of numerous closely spaced fine spiral cordlets alternating in strength and somewhat scaly; cordlets strongest at and near periphery where two or three can be stronger becoming cords and the scales bead-like, with approximately three cordlets in interspaces; aperture ovoid, its abapertural margin sharply demarked and steeply descending; inner lip and columella flattened and expanded to form shelf; shelf narrow anteriorly becoming moderately wide medially, submerged within aperture, wrapping past suture and attached to inside of outer lip.

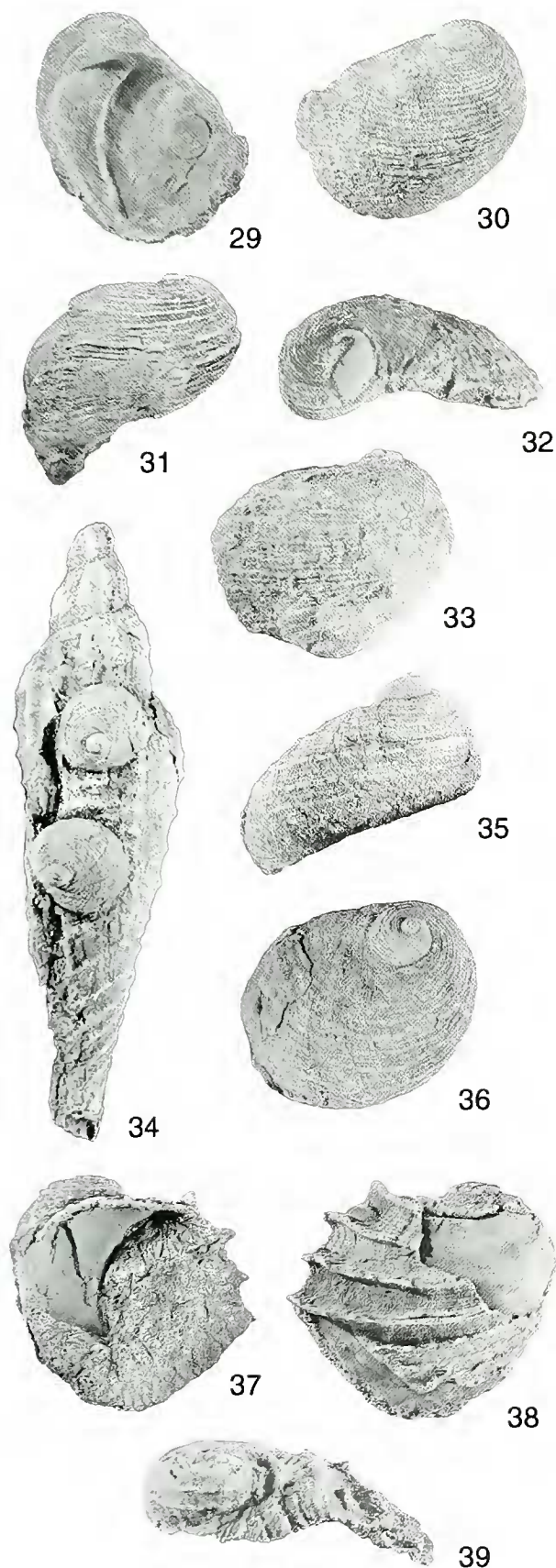
**Holotype:** LACMIP 13386, height approximately 35 mm, diameter 34 mm.

**Paratypes:** LACMIP 13387 (LACMIP loc. 24137)–13388 (LACMIP loc. 24122) and SDNHM 114595, 114596 (SDNHM loc. 3405).

**Type Locality:** LACMIP loc. 24137, Jalama Formation.

**Figures 29–39.** *Lysis* species. Specimens coated with ammonium chloride. **29–36.** *Lysis jalamaca* new species. **29–30.** Holotype LACMIP 13386, LACMIP loc. 24137. **29.** Apertural view, vertical dimension 34 mm, horizontal dimension 30 mm. **30.** Abapertural view, vertical dimension 27 mm, diameter 34 mm. **31–32.** Paratype LACMIP 13387, LACMIP loc. 24137. **31.** Left-lateral view, height 15 mm, horizontal dimension 19 mm. **32.** Lateral view, vertical dimension 11.5 mm, diameter 28 mm. **33.** Paratype LACMIP 13388, LACMIP loc. 24122, abapertural view, height 11 mm, diameter 13 mm. **34.** Paratypes SDNHM 114595 and 114596, SDNHM loc. 3405 on outer lip of volute gastropod *Longoconcha eumeka* Saul and Squires, 2008 (SDNHM 70974), SDNHM loc. 3405, height 133 mm, diameter 33 mm. **35–36.** Posterior-most paratype SDNHM 114596 on volute shown in previous figure. **35.** Abapertural view, height 13 mm, diameter 20 mm. **36.** Oblique apical view, vertical dimension 17 mm, diameter 20 mm. **37–39.** *Lysis lomaensis* new species, holotype SDNHM 67150, SDNHM loc. 3403, height 22 mm, diameter 23 mm. **37.** Apertural view. **38.** Abapertural view. **39.** Apical/lateral view, vertical dimension 8 mm, diameter 23 mm.





**Distribution:** Jalama Formation, (area 12) western Santa Ynez Mountains, Santa Barbara Co.; Debris Dam Sandstone, (area 13) Agua Caliente Canyon, San Rafael Mountains, Santa Barbara Co., California; Chatsworth Formation, upper part (area 16) at Lang Ranch, Ventura Co., California; Point Loma Formation, (area 19) near Carlsbad, San Diego Co., California; Rosario Formation, (area 22) Cañon San Fernando, northwestern Baja California, Mexico.

**Geologic Age:** Late Campanian and early Maastrichtian.

**Discussion:** The above description is based on 13 specimens. The best preservation occurs in the Point Loma Formation near Carlsbad.

*Lysis jalamaca* is similar to *L. suciensis* but has coarser, more scaly costae than *L. suciensis*, and available specimens of *L. jalamaca* are smaller and less elongate than are large specimens of *L. suciensis*. *Lysis jalamaca* is also similar to *L. duplicosta* in having variable sculpture and in having the strongest cords on the periphery, but *L. jalamaca* is less angulate at the periphery and has weaker cords there. In addition, *L. jalamaca* differs from *L. duplicosta* by being more elongate, having finer sculpture, and having the shelf broader posteriorly. The specimen (LACMIP 13378, Figures 18, 19) from the Jalama Formation has ribbing similar to *L. duplicosta*, but its shelf appears to wrap farther onto the interior of the outer whorl than is usual for *L. duplicosta*.

**Etymology:** The specific epithet, a name in apposition, reflects the new species occurrence in the Jalama Formation, Santa Barbara Co., California.

*Lysis lomacensis* new species  
(Figures 37–39)

**Diagnosis:** *Lysis* with low spire and last whorl bearing numerous flanged carinae separated by wide interspaces bearing several spiral threads.

**Description:** Shell medium size (up to 17 mm height and 30 mm diameter, same specimen), neritiform (last whorl rapidly expanding); spire very low, approximately 10 to 15% of shell height; protoconch 1.5 whorls, low and smooth; teleoconch 2 to 2.5 whorls, very carinated; suture abutting just anterior to periphery; sculpture consisting of up to 11 strong cords; cord at periphery and next three cords posterior of periphery very thin, flanged, and protruding (with cord at periphery protruding most); posteriormost part of last whorl (in vicinity of suture) with approximately three low scaly cordlets; up to three beaded to lowly spinose cordlets anterior to medial carina at periphery; interspaces between all cords wide and bearing up to seven spiral threads (occasional thread can locally develop into small flanged cord); area anterior to medial carina can be covered with only fine cordlets; aperture circular with margin sharply demarked by raised edge; shelf moderately wide, wrapping past suture and attached to inside of outer lip; posterior half of outer lip digitate.



**Holotype:** SDNHM 67150, height 22 mm, diameter 23 mm.

**Paratype:** SDNHM 67152 from SDNHM loc. 4071.

**Type Locality:** SDNHM loc. 3403.

**Distribution:** Basal San Francisquito Formation, (area 14) Warm Springs Mountain, Los Angeles Co.; Point Loma Formation, (area 19) San Diego Co., California; Rosario Formation, (area 21) five miles east of La Misión, northwestern Baja California, Mexico.

**Geologic Age:** Latest Campanian to late Maastrichtian.

**Discussion:** Five specimens were studied. Preservation is generally excellent for three specimens from the Point Loma Formation near Carlsbad, although the protoconch of the holotype is imperfectly preserved. The incomplete, crushed specimen from Warm Springs Mountain is from beds of latest Maastrichtian age at the base of the San Francisquito Formation (LACMIP loc.

14310). Although the abapertural side is not available, the flatness of the apical whorls suggests that it is probably *L. lomaensis*.

The new species is most similar to *Lysis duplicosta* but available specimens are smaller than a large *L. duplicosta*. *Lysis lomaensis* also has a lower spire, more carinate last whorl (especially posterior to the medial carina), and spiral threads on interspaces between carinae.

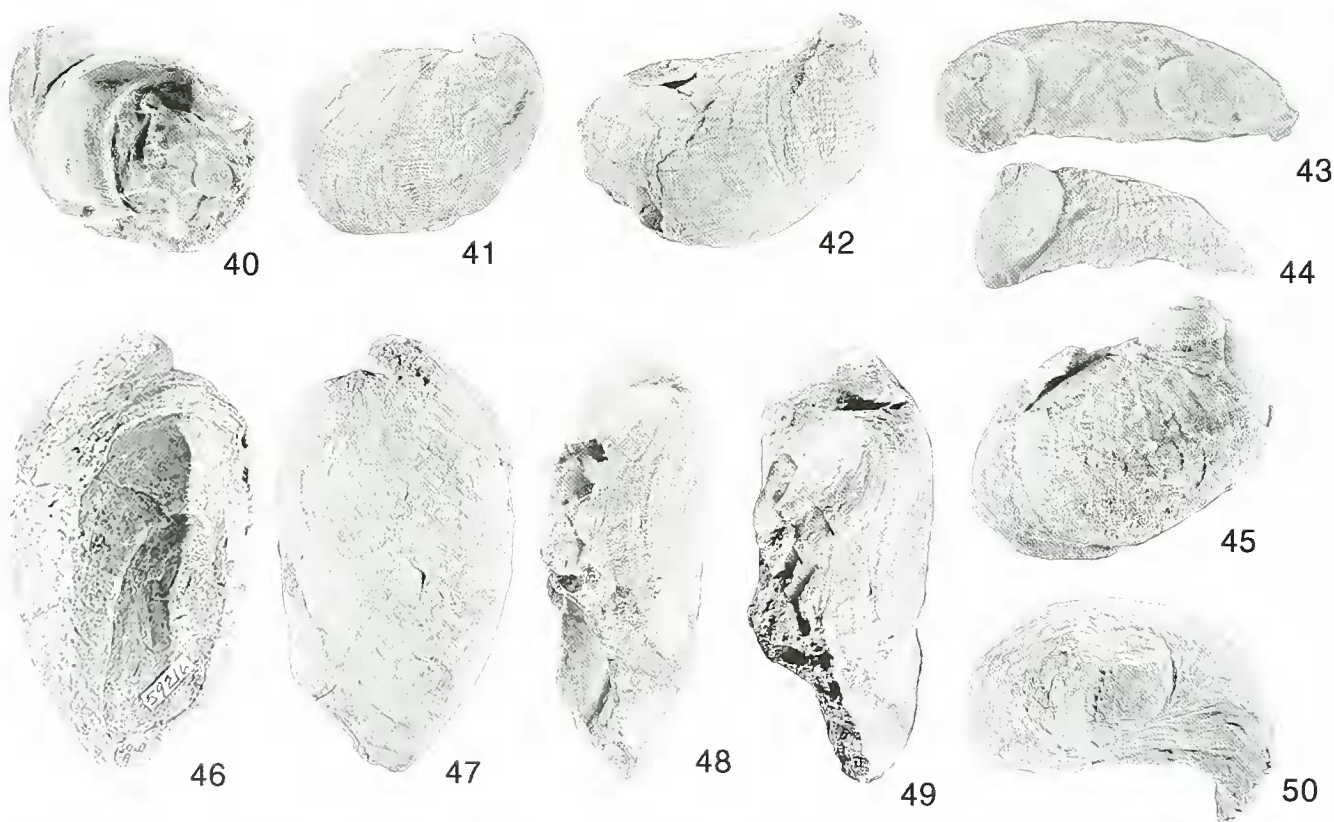
Abaperturally, *L. lomaensis* is similar in shape and sculpture to *Garzasia intermedia*, but *L. lomaensis* has a lower spire and in the apertural view the shelf margin is less arcuate, not sigmoid, and the shelf does not spiral into the umbilicus.

#### Group of *Lysis suciensis*

The group of *L. suciensis* differs from that of *L. duplicosta* in having a more elongate aperture and finer spiral sculpture.

*Lysis suciensis* (Whiteaves, 1879)

(Figures 40–50)



**Figures 40–50.** *Lysis suciensis* (Whiteaves, 1879). Specimens coated with ammonium chloride. **40–41.** Hypotype LACMIP 13359, LACMIP loc. 26020. **40.** Apertural view, vertical dimension 44 mm, horizontal dimension 40 mm. **41.** Abapertural view, height 25 mm, diameter 43 mm. **42–43.** Hypotype LACMIP 13390, LACMIP loc. 10711. **42.** Abapertural view, height 18 mm, diameter 26.5 mm. **43.** Lateral view, vertical dimension 8 mm, diameter 26.5 mm. **44.** Hypotype LACMIP 13391, LACMIP loc. 10095, lateral view, vertical dimension 5 mm, diameter 12.5 mm. **45.** Hypotype LACMIP 13392, Cañon San Fernando, 32 km southeast of El Rosario, Baja California, Mexico, abapertural view, height 15 mm, diameter 21 mm. **46–50.** Hypotype LACMIP 10495, LACMIP loc. 26020. **46–47.** Vertical dimension 70 mm, horizontal dimension 38 mm. **46.** Apertural view. **47.** Abapertural view. **48.** Right-lateral view, vertical dimension 70 mm, horizontal dimension 25 mm. **49.** Slightly oblique right-lateral view, vertical dimension 70 mm, horizontal dimension 27 mm. **50.** Lateral view, vertical dimension 25 mm, horizontal dimension 36 mm.

*Stomatia suciensis* Whiteaves, 1879: 128–129, pl. 16, fig. 4.  
*Lysis suciensis* (Whiteaves).—Whiteaves, 1903: 367, pl. 45, fig. 3. Stecheson, 2004: 60–62, pl. 2, figs. 4–5.  
*Lysis californiensis* Packard, 1922: 431, pl. 37, figs. 2–3; Staudum, 1973: pl. 2, fig. 12.  
*Lysis duplicosta* Gabb.—Saul and Alderson, 1981: 36, pl. 3, figs. 3–4. Not *Lysis duplicosta* Gabb, 1864.

**Diagnosis:** Medium to large *Lysis*, shell elongate with fine, usually wavy cordlets, sculpture obsolete on large specimens.

**Description:** Medium to large (height up to 84 mm), crepiduliform, elongately expanded; spire moderately high to low, approaching horizontal coiling, and approximately 30 to 35% of total shell height; protoconch approximately 1 to 1.5 whorls, low and smooth; teleoconch approximately 1.5 to 2 whorls, whorls subcarinate to rounded; periphery near one-third whorl height; suture abutting just anterior to periphery, descending; growth line slightly to moderately parasigmoidal, with sinus at posterior end of outer lip on large, smooth individuals; sculpture consisting of fine narrow cordlets, usually wavy, alternating in strength, with narrow interspaces; aperture elongate ovoid, its abapertural margin sharply demarked and steeply descending; inner lip and columella flattened and expanded to form crescentic and moderately wide deck submerged within aperture, posterior end attached to inside of outer lip; inner deck margin concavely curved.

**Syntypes:** Of *Stomatia suciensis* CGS 5771, a–d.

**Lectotype** (here chosen): Of *Stomatia suciensis* CGS 5771, height 66 mm.

**Paralectotypes:** Of *Stomatia suciensis* CGS 5771a–CGS 5771d.

**Holotype:** Of *Lysis californiensis* UCMP 12287.

**Paratype:** Of *Lysis californiensis* UCMP 12288.

**Type Locality:** *Stomatia suciensis*, Sucia Island, San Juan Co., Washington. Of *Lysis californiensis*, UCMP loc. 2167, Santa Ana Mountains, Orange Co., California.

**Figured Specimens:** LACMIP 10495, 13389, from LACMIP loc. 26020; LACMIP 13390 from LACMIP loc. 10711; LACMIP 13391 from LACMIP loc. 10095; LACMIP 13392 from the Rosario Formation, (area 22) 26 km east of coastline at elevation 200 m on west side of Cañon San Fernando, 15 km north of Mesa San Carlos, approximately 32 km. southeast of El Rosario, Baja California, Mexico.

**Distribution:** Upper Cedar District Formation, (area 1) Denman Island, Gulf Islands, British Columbia; Lower Cedar District Formation, (area 2) Sucia Island, San Juan Co., Washington; Chico Formation, (area 7) Granite Bay, Placer Co.; Jalama Formation, (area 12) western Santa Ynez Mountains, Santa Barbara Co.; Chatsworth Formation, (area 16) Bell Canyon and Dayton Canyon, Simi Hills, Ventura Co., California; Ladd Formation, upper Holz Shale Member, (area 18) Santa Ana

Mountains, Orange Co., California; Rosario Formation (area 22) at Cañon San Fernando, 26 km SE of El Rosario Baja California; Valle Formation, (area 23) 10 km north from Punta Abreojos, Baja California Sur, Mexico.

**Geologic Age:** Late early Campanian and early Maastichtian.

**Discussion:** The above description was based on 107 specimens. The deck of smaller specimens is rather narrow and attaches to the base of the previous whorl. Small specimens are rounded, larger specimens more elongate. In larger specimens the shelf is broader and its posterior end attaches to the inside of the outer lip. Several specimens, especially the larger specimens, have an obtusely biangulate whorl apical to the periphery. Most specimens from Sucia Island are of small size and badly weathered, but Whiteaves's largest specimen (1879: 129, pl. 16, fig. 4), here designated as lectotype, was indicated by him to be "two inches and a half in length" (i.e., 66 mm). The specimen from Bell Canyon (area 16) of Figures 46–50, lacking its spire and with its outer lip broken, is 75 mm high.

The ribbing on larger specimens from the Chatsworth Formation in Bell and Dayton canyons, Simi Hills (area 16) tends to become fainter toward the outer lip especially on the posterior slope. The specimen figured (Figures 40, 41) retains ribbing around the periphery, but the ribs fade posteriorly toward the aperture. Height range of the smoother specimens is 45 to 76 mm (incomplete), making these the largest specimens thus far found of *Lysis*. The largest of these specimens are larger than representatives of most species of *Crepidula*; only *Grandicrepidula princeps* (Conrad, 1856), attains a larger size.

Genus *Garzasia* new genus

**Type Species:** *Garzasia diabla* new species from the "Garzas Sand" Member of the Moreno Formation, Stanislaus Co., California; mid Maastichtian.

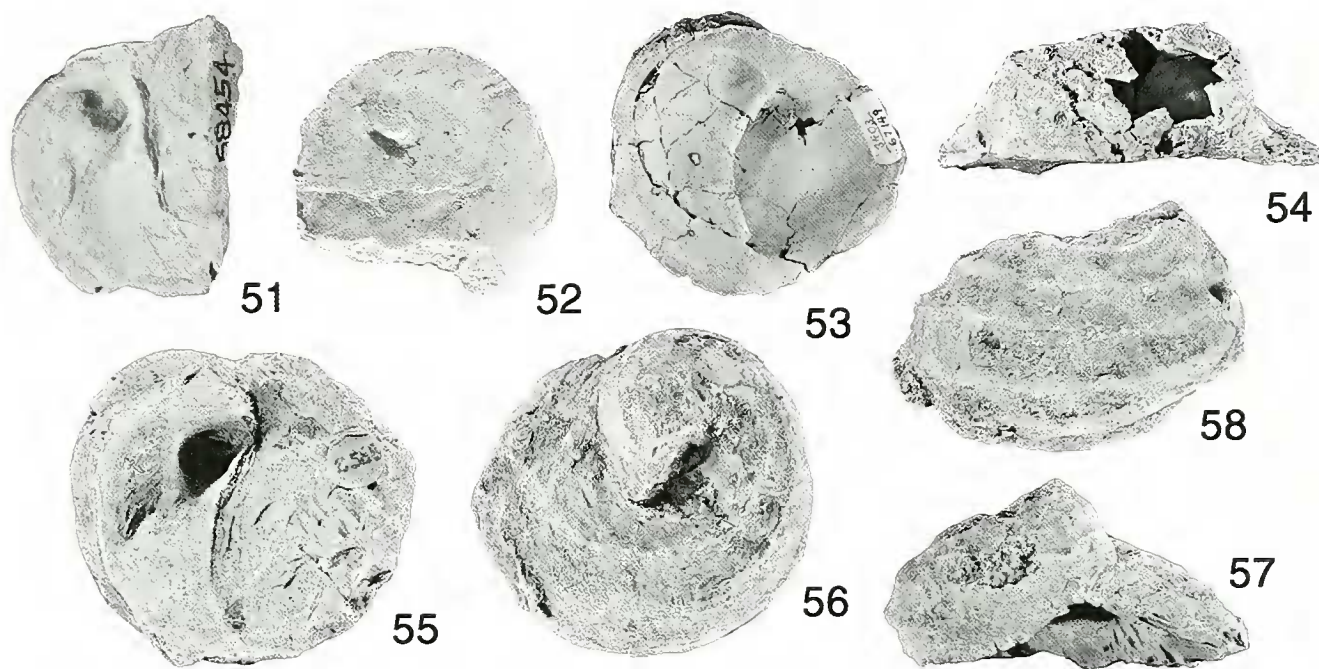
**Description:** Very low to moderately high spired, *Calyptrea*-like shell with weak to strong spiral cords, aperture very broadly expanded and forming base of shell, shelf attached marginally, surrounding the umbilicus, and spiralling into it.

**Discussion:** *Garzasia* is most similar to *Lysis* but differs from the latter in that the deck surrounds and spirals into an umbilicus somewhat as in *Calyptrea* but with a wider more open umbilicus. It differs from *Calyptrea* in having a sturdier shelf attached marginally as in *Trochita*. It differs from *Trochita* (Figure 71) in having the shelf crescentic with an arcuate to slightly sigmoidal shelfal edge, the axis of spiraling of its shelf off center, and external ribbing spiral rather than protractive.

**Etymology:** The genus *Garzasia* is named for the "Garzas Sand" and Garzas Creek, Stanislaus Co., California.

*Garzasia intermedia* (Cooper, 1894)  
 (Figures 51–54)





**Figures 51–58.** Species of *Garzasia* new genus. **51–54.** *Garzasia intermedius* (Cooper, 1894). **51–52.** Plasto-lectotype of CASG 609, Point Loma Formation. **51.** Apertural view, vertical dimension 21.5 mm. **52.** Apical view, diameter 19 mm. **53–54.** Hypotype SDSNH 67149, SDSNH loc. 3403. **53.** Apertural view, vertical dimension 61.5 mm, diameter 64 mm. **54.** Left-lateral view of spire above posterior part of aperture, height 20 mm, diameter 64 mm. **55–58.** *Garzasia diabla* new species. **55–57.** Holotype LACMIP 13393, LACMIP loc. 22588. **55.** Apertural view, vertical dimension 36 mm, diameter 37 mm. **56.** Abapertural view, vertical dimension 34 mm, diameter 37 mm. **57.** Side view of spire above posterior part of aperture, height 18 mm, diameter 37 mm. **58.** Paratype LACMIP 13394, LACMIP loc. 26353, slightly oblique left-lateral view (partial specimen), height 29 mm, diameter 9 mm.

*Stomatia intermedius* Cooper, 1894: 46, pl. 3, fig. 43 [refigured in Yates, 1903: pl. 3, fig. 43].

*Lysis intermedius* (Cooper).—Anderson, 1955: 170; Coan, 1951: 165, fig. 12 [reprint of Cooper's pl. 3].

**Diagnosis:** Large *Garzasia*, haliotiform, carinate on periphery, sculpture elsewhere consisting of several low spiral cords separated by wide interspaces bearing up to 10 spiral threads, shelf very broad, with arcuate to slightly signoidal margin.

**Description:** Large size (height up to 37 mm, diameter 68 mm, same specimen); haliotiform with very rapidly expanding last whorl; protoconch unknown; spire highly variable in elevation, ranging from 50 to 85% of total shell height; suture abutting below periphery; growth line prosocline; sculpture consisting of commonly five spiral cords; periphery carinate and bearing strongest cord; peripheral carina located anteriorly of medial position on spire whorl but medially on last whorl; adapical to medial carina two to three medium-strong cords with wide interspaces bearing up to 10 spiral threads; just abapical to medial carina several closely spaced and scaly medium strong cords; aperture circular; inner lip and columella flattened to slightly concave and expanded to form very wide crescentic shell submerged within aperture; posterior end of shelf surrounds umbilicus and spirals into it.

**Lectotype:** CAS 609 (formerly CSMB 13742), height 6.4 mm, diameter 22.6 mm (incomplete).

**Type Locality:** Point Loma, San Diego Co., California.

**Figured Specimen:** SDSNH 67149 from SDSNH 3403.

**Distribution:** Point Loma Formation, (area 19 and 20) San Diego Co., California.

**Geologic Age:** Latest Campanian and early Maastichtian, *Baculites lomaensis* zone.

**Discussion:** The above description was based on six specimens, of which preservation is generally good to excellent.

Cooper's (1894) figure 43 line drawing is actually a combination of three specimens. The lectotype (CASG 609) is designated by us and is photographed here (Figure 51) for the first time.

*Garzasia intermedius* differs from *G. diabla* new species in achieving larger size, having weaker carinae with the medial carina being most prominent, and having spiral threads in interspaces between carinae.

*Garzasia intermedius* is somewhat similar to *Sigapatella* Lesson, 1830, some species of which [e.g., *Sigapatella novaezelandiae* (Lesson, 1830)] have spiral sculpture, an off-centered apex, and a well-developed "false" umbili-



cus. The umbilicus of *Garzasia* appears to form as the widely expanded, flattened columella is attached medially around the axis of coiling forming a broad shelfal area. In the holotype of *G. intermedia* and some other specimens this area is an open, funnel shape, but in others the area is more or less filled, resulting in shelves with differing "umbilical" development from a moderate to deep depression. The shelfal edge of *Garzasia* differs from that of *Sigapatella* in being sigmoidal rather than arcuate.

A large specimen SDNHM 67149/3403 has faint markings at each end of the shelf which resemble muscle scars.

*Garzasia diabla* new species  
(Figures 55–58)

**Diagnosis:** Medium sized, *Calypttraca*-like, with moderately high spire, having three to four equal-strength carinate ribs with wide interspaces.

**Description:** Medium to moderately large size (up to 30 mm in height), *Calypttraca*-like shell with rapidly expanding last whorl; spire moderately high, approximately 40 to 50% of total shell height; protoconch missing; teleoconch approximately 1.5 whorls, carinate; periphery near one-half whorl height; suture abutting at periphery; sculpture consisting generally of three to four equal-strength and equally spaced carinae with very wide interspaces; aperture circular with its abapertural margin sharply demarked and steeply descending; inner lip margin slightly sigmoidal; posterior end attached to inside of outer lip directly beneath suture; shelf spiraling into umbilicus.

**Holotype:** LACMIP 13393, height 18 mm, diameter 37 mm.

**Paratype:** LACMIP 13394 from LACMIP loc. 26353.

**Type Locality:** LACMIP loc. 22588.

**Distribution:** Moreno Formation, "Garzas Sand" Member, (area 9 and 10) Merced and Stanislaus counties, California.

**Geologic Age:** "Mid" Maastrichtian.

**Etymology:** The species is named for its occurrence in the eastern foothills of the Diablo Range, Merced and Stanislaus counties, California. The specific epithet *diabla* is used as a name in apposition.

**Discussion:** The above description is based on eight specimens. Preservation of the known specimens of this species is poor. Except for the holotype, all the specimens are internal molds.

This species is very similar to *G. intermedia* from which it differs in having a generally lower but more roundly inflated, spire that is apparently not variable in height, higher last whorl, much stronger sculpture, and the basal flange wrap into the aperture to meet the apertural edge of the shelf.

## EVOLUTIONARY IMPLICATIONS

The presence of both fine-ribbed and coarse-ribbed *Ariadnaria* and *Lysis* suggests that species of *Lysis* may have been derived from *Ariadnaria*. During the evolution of *Lysis*, the inner lip broadened (as did the columella) and apparently moved deeper into the aperture, thereby allowing more room for the foot to grasp hard substrate. These changes, assumed to be a function of the rapid expansion of the aperture, were necessary in order that the aperture could accommodate a larger foot for attachment to a hard substrate. The resultant shell shape was crepiduliform. Modern trichotropids studied by Yonge (1962) in Puget Sound thrive on unstable shell beds. If some Cretaceous trichotropids resembled the modern trichotropids in (1) being filter feeders, (2) living on firm substrates, and (3) being protandrous hermaphrodites, they would have had characteristics that allowed them to evolve toward the less vagile calyptraeids or crepidulids.

The inner lip of trichotropids is homologous to the internal deck or shelf of calyptraeids, and the development of the shelf in *Lysis* serves as a pattern for the development of the flat shelf in *Crepidula* Lamarck, 1799, and of the shelf in *Garzasia* for the spiral shelf in *Calypttraca* Lamarck, 1799. Trichotropid and crepidulid sculpture is predominantly spiral (i.e., in the direction of coiling), but some calyptraeid sculpture is radial or protractive.

The shell exterior of *Lysis suciensis* group (i.e., *Lysis suciensis* lineage) is fine-ribbed to relatively smooth; interiorly the columella and inner lip are flattened and broadened into a crescentic shelf which, as it lengthened posteriorly, came to resemble a shelf of *Crepidula*. Except for its large size, *Lysis suciensis* resembles the earliest species from the Pacific slope usually assigned to *Crepidula*; namely, '*Crepidula*' *pileum* (Gabb, 1864), which ranges from middle Eocene to Oligocene in California to Washington. Stewart (1927) and Hoagland (1977) slightly extended the range of '*C.*' (*Spirocrypta*) *pileum* by synonymizing with it the late early Eocene *Spirocrypta inornata* (Dickerson, 1916) and the middle to late Eocene *Spirocrypta dickersoni* (Weaver and Palmer, 1922), but Vokes (1939) considered *Spirocrypta inornata* of "Domengine" age to have "a funnel-like process due to the upward curving of the posterior portion of the septa" (Vokes, 1939, pl. 13, fig. 7) rather than the less apparent "umbilicus" of *S. pileum* (see discussion below).

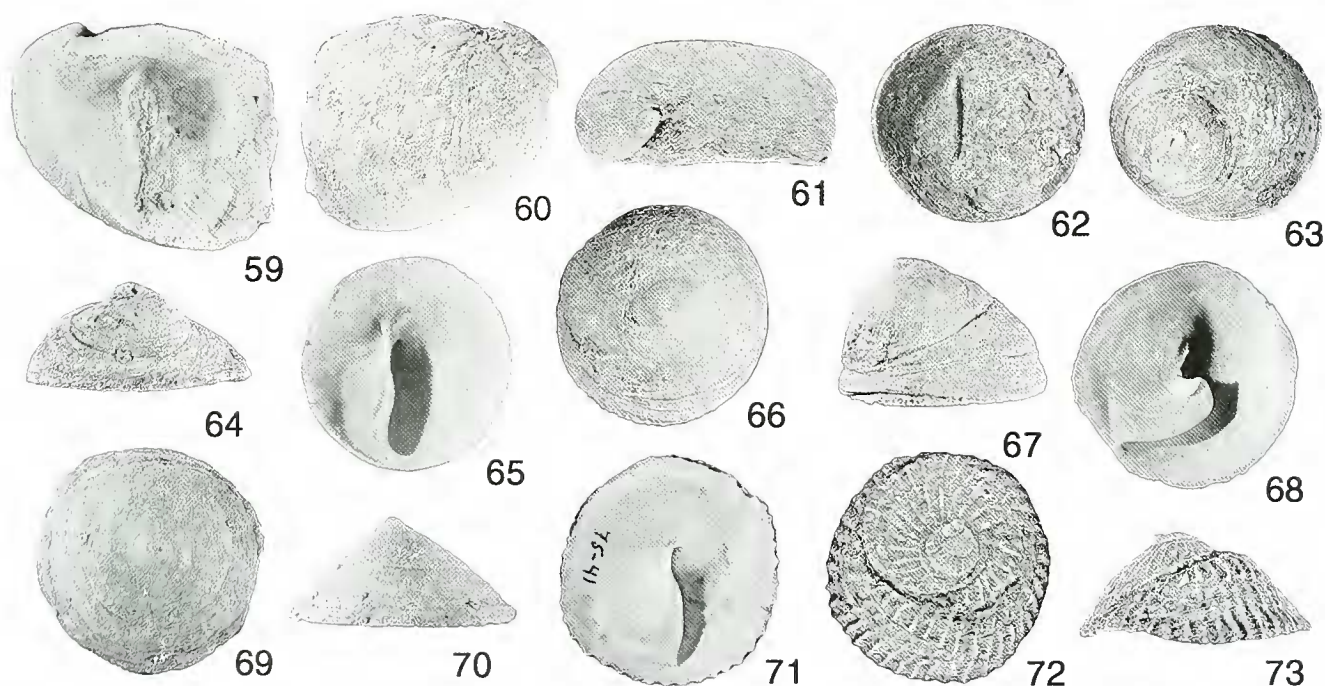
Gabb (1864) originally placed '*Crepidula*' *pileum* in the invalid genus *Crypta* Humphrey, 1797 (a synonym of *Crepidula*), and subgenus *Spirocrypta* Gabb, 1864, of which '*C.*' (*S.*) *pileum* is the type species. '*Crepidula*' (*S.*) *pileum*, which is common in the Tejon Formation of middle Eocene age in Live Oak Canyon, Kern Co., California, has been figured several times (e. g., Gabb, 1864: pl. 29, figs. 233, 233a–b; Stewart, 1927: pl. 29, figs. 2–3; Anderson and Hanna, 1925: pl. 13, fig. 7; Clark, 1938: pl. 4, fig. 19; Wenz, 1940: figs. 2660a, b [reprint of Stewart]). A large specimen from the late Eocene is figured by

Kleinpell and Weaver (1963, pl. 24, fig. 11). Weaver's (1943: 724, pl. 71, fig. 16) illustration of *Calyptrea diegoana* (Conrad) is a lapsus and is a posterior-end-up, apertural view of '*Crepidula pileum*'. On page 356 he correctly lists the figure as *Crepidula pileum*. Gabb's (1864: pl. 29, fig. 233a) and Stewart's (1927, pl. 29, fig. 3) show the shelf. Gabb's figure is a facsimile and Stewart's is a photograph that has been reproduced in other discussions of *Spirocrypta* (e.g., Wenz, 1940: 903, fig. 2660a). Gabb's and Stewart's figures are based on lectotype ANSP 4221, but, unfortunately, the shelf of this specimen is broken. Both figures create the false impression that there is a sinus near both ends of the shelf and that the middle part protrudes and is concave. An additional representative specimen (hypotype LACMIP 13395) was cleaned by the senior author and is illustrated in Figures 59–61. Its shelf (Figure 59), which is unbroken, is slightly sigmoidal and long on the left side (or anterior end) and shorter on the right side (or posterior end). There is also a slight convexity of the somewhat sinuous shelf as it approaches the posterior end of the aperture and the shelf margin spirals over slightly to form an indication of an umbilicus. In addition, the shelf is also narrower and closer to the shell margin on the left/

anterior and noticeably farther from the shell margin (deeper into the aperture) on the right/posterior. The shelf of '*C. pileum*' thus, as noted by Gabb (1864), spirals inward toward the apex. Gabb's figure (pl. 29, fig. 233b) in part illustrates this, as does Figure 59. Although Stewart (1927) synonymized *Spirocrypta* with *Crepidula*, Gabb's description of *Spirocrypta* recognizes this very important characteristic, which helps to distinguish *Spirocrypta* from *Crepidula*. In modern *Crepidula fornicata*, the shelf does not spiral into the whorl apex.

Aperture/shelf features of *Spirocrypta pileum* and *S. inornata* resemble those of the early Paleocene *Spirogalenus lamellaria* Finlay and Marwick, 1937, from New Zealand, in that the shelf of *S. lamellaria* is also narrower and closer to the shell margin on the left/anterior and noticeably farther from the shell margin (deeper into the aperture) on the right/posterior.

Our proposed evolutionary relationship between trichotropines and calyptraeids differs from any previous author's proposal. Hoagland (1977), for example, in her study of *Crepidula* Lamarck, 1799, rejected trichotropids as direct ancestors of calyptraeids and crepidulids. Hoagland (1977) opined that although *Trichotropis* Broderip and Sowerby, 1829, and *Crepidula* had a common an-



**Figures 59–73.** Fossil Calyptraeidae. 59–64. Comparative Eocene *Crepidula* and *Calyptrea* species. 59–61. *Spirocrypta pileum* (Gabb, 1864), hypotype LACMIP 13395, LACMIP loc. 22386, vertical dimension 3 mm, diameter 9 mm. 59. Apertural view. 60. Abapertural view. 61. Lateral view. 62–64. '*Calyptrea*' *diegoana* (Conrad, 1855), hypotype LACMIP 13458, LACMIP loc. 22340. 62. Apertural view, vertical dimension 29 mm, diameter 31 mm. 63. Apical view, diameter 31 mm. 64. Right lateral view, height 13 mm, diameter 31 mm. 65–67. '*Calyptrea*' *aperta* Solander in Brander, 1766, hypotype LACMIP 13396, LACMIP loc. 7333. 65. Apertural view, vertical dimension 11 mm, diameter 11 mm. 66. Apical view, diameter 11 mm. 67. Right-lateral view, height 7 mm, diameter 11 mm. 68–70. *Calyptrea chinensis* (Linnæus, 1758), Recent, type-species, hypotype LACM 161651, Cherbourg (Manche), Normandie, France. 68. Apertural view, vertical dimension 15 mm, diameter 14.5 mm. 69. Apical view, diameter 14.5 mm. 70. Right-lateral view, height 6 mm, diameter 14.5 mm. 71–73. *Trochita trochiformis* (Born, 1778), Recent, type-species, LACM loc. lot 75–41, Punalu, west of Isla Telcon, Gulf of Corcovado, Chiloe Province, Chile – intertidal. 71. Apertural view, vertical dimension 40 mm, diameter 38 mm. 72. Apical view, diameter 38 mm. 73. Right-lateral view, height 18 mm.



cestor, *Trichotropis* has no direct relationship to *Crepidula* because *Trichotropis* is boreal, living in cold and deep water and has rough sculpture, whereas *Crepidula* had its origin in the Panamic region and is relatively smooth sculptured. Her implications that *Trichotropis* is a deep, cold-water gastropod and that *Crepidula* is a shallow, warm-water gastropod are misleading. Modern *Trichotropis cancellata* (Hinds, 1843) is intertidal in Alaska, British Columbia, and Washington to depths of 104 m off Alaska, 165 m off British Columbia, and 274 m off Washington (LACM Malacology collection). In the southern part of *T. cancellata*'s range, it is in cool-temperate, not boreal waters. The question is, however, not where trichotropids live now but where they were during the Late Cretaceous, when there were no polar ice caps and the subtropical and temperate zones were much wider. Trichotropids and calyptraeid-like gastropods co-existed during the Late Cretaceous in the study area, and both forms lived in relatively warm, shallow waters. Although the Coniacian-Santonian faunas of northern California are noticeably cooler than Turonian faunas (Saul and Squires, 2008) of that area, they would have been temperate. Hoagland (1977) mentioned that anatomical features of *Trichotropis* suggest affinities to calyptraeids, but she believed that similarities of life history and niche between *Trichotropis* and *Crepidula* are convergent. She suggested that *Crepidula* is derived from some form of "calyptraeid stock" that, in turn, was derived from *Trochita* Schumacher, 1817, reported by Wenz (1940) to range from Eocene to Recent. She did not provide any geologic time parameters as to when these derivations took place, but indicated that Shimer and Shrock (1959) recorded the first calyptraeids as "lower Cretaceous." The "lower" seems to be a minor lapsus: all printings of Shimer and Shrock from first 1944 to last 1959 list range of *Calyptraca* and *Crepidula* as "U. Cret.-Recent" and *Crucibulum* as "Tert.-Recent." Wenz (1940: 902), however, questionably included the peculiar looking genus *Galericulus* Seeley, 1861 from the Upper Greensand (Lower Cretaceous upper Albian) of England in calyptraeids. It does not resemble any calyptraeid we have studied. Seeley (1861) named *Crepidula cooksoniae* also from the Upper Greensand, but Hoagland (1977: 395) found it "unconvincing" as a calyptraeid.

The Campanian to Maastrichtian *Damesia* Holzapfel, 1855, of Europe and Tennessee, has been regarded as a calyptraeid by some workers (e.g., Sohl, 1960), but Dockery (1993) assigned *Damesia* to the pyramidelloids.

Bandel and Riedel (1994) reviewed placement and content of Calyptraeidea, and in comparison to Hoagland's (1977) study, they arrived at a different familial content and different relationships between the families. Their Calyptraeidea consisted of two families: Calyptraeidae containing genera *Calyptraca*, *Crucibulum*, and *Crepidula*; and Hipponicidae containing *Cheilea*, *Hipponix*, *Neojanaca*, and *Thylacus*; but both families excluded trichotropids. According to Bandel and Riedel (1994), all genera in Calyptraeidae lack a proboscis and

are obligatory filter feeders. However, in Hawaii Ulbrich (1969) reported algae grazing, in addition to filter feeding by *Crucibulum spinosum* Sowerby, 1824.

Cretaceous trichotropines probably had several characteristics that lysines would have inherited from them: 1) filter feeding, 2) living epifaunally, probably on a hard substrate, 3) brooding egg capsules from which planktotrophic larvae hatch, and 4) being protandrous hermaphrodites. Characteristics the lysines would pass on to calyptraeids. Lysines' first recognizable difference from the trichotropines is the increase in expansion rate of the whorl, especially of the last whorl, resulting in an enlarged aperture in which the columella is broadened. The earliest broadening and enlargement were moderate and only become striking as geologically younger species began to have a very distinctive morphology. Until connected with its ancestry, *Lysis* was difficult to classify. The shell also became more flattened and limpet-like, as the aperture enlarged.

Hoagland (1977) credited *Crepidula hochstetteriana* Wilkens (1922: 5-6, pl. 1, figs. 9a, b) as being the earliest *Crepidula* because it was reported from the calcareous conglomerate stratigraphic unit of the Lower "Amuri Group" in the "Amuri Bluff" area, northeastern South Island, New Zealand (Wilkens, 1922; Warren and Speden, 1978). Modern spelling of "Amuri" is Haumuri, and the Cretaceous strata are referred to the Mata Series. Woods (1917) reported that these strata at Haumuri Bluff contain the bivalves *Inoceramus australis* Woods, 1917 and *Inoceramus pacificus* Woods, 1917, which according to Wellman (1959) are limited to the Piripauan Stage of latest Coniacian to Santonian age.

Warren and Speden (1978) noted "problems" with the early collections from this area but nevertheless, listed *Maoricrypta hochstetteriana* (Wilkens, 1922) from the Campanian Okarua Sandstone of the Mata Series. Described conditions of collecting suggested a strong possibility of co-mingling of material from different strata and that the only known specimens of *M. hochstetteriana* might not be from the Mata Series. In search of the type specimen, we contacted three extraordinarily helpful New Zealanders: A. G. Beu, A. Grebneff, and J. D. Stilwell. Their email communications (2006) indicated that *M. hochstetteriana* is not from the Okarua Sandstone, and is not of Cretaceous age. Beu found the type specimen (GNS TM2608) in the New Zealand Geological Survey collections. Fortunately, the type specimen was in a large enough block of matrix to take a sample for microfossil dating. He enlisted the aid of G. Wilson who dated the dinoflagellates as late Oligocene, at the oldest. Ian Raine, who looked at the rich spore-pollen assemblage also from the sample, found *Acacia* pollen, which is not known earlier than Miocene in New Zealand. Miocene strata crop out above the Mata Series, and some of the original material sent to Wilkens was apparently from beach boulders derived from younger strata overlying the Cretaceous Mata Series. This Neogene age for Wilkens' species is much more likely considering that the shell



covers nearly one-half of the aperture (Hoagland, 1977: 380).

Hoagland published more papers on *Crepidula* and, in 1986, she revised several items of her 1977 paper but did not design a new evolutionary pathway. We differ from Hoagland (1977) in that we believe it is difficult to go from the centrally oriented apex plan of *Trochita* (Figure 71) or *Calyptrea* (Figure 68) with its spiraling shelf and get to *Crepidula* with its eccentric spire and apparently unspiraled deck. Whether or not *Lysis* species are ancestral to any modern *Crepidula*, younger species of *Lysis* achieved a crepiduloid form with a respectable shelf by wrapping the posterior end of the shelf onto the inside of the outer whorl. Furthermore, from this, the calyptraeid form appears to have evolved with the development of an "umbilicus" in *Garzasia intermedia* making Cooper's specific name remarkably prescient.

At about the Campanian/Maastrichtian boundary, development of the spiral shelf of *Garzasia* resulted in a shelf that appears to be a pattern for development of shelves in *Calyptrea* and perhaps *Crucibulum*. The very broad, depressed spiraling inner lip of *Garzasia* appears to provide a likely pattern for development of the shelf of *Calyptrea* or *Crucibulum*, not for the more decklike shelf of *Crepidula*.

The earliest reported *Calyptrea* on the Pacific slope is '*Calyptrea*' *diegoana* (Conrad, 1855) which ranges from middle Paleocene to Oligocene and occurs from California to Washington and easternmost Russia (Squires, 1987). A representative specimen from the Tejon Formation Eocene is shown in Figures 62–64. Figure 62 displays the shelf of this species, which is similar to that of '*Calyptrea*' *aperta* Solander in Brander, 1766 from the Eocene of Europe (Figures 65–67). Both of these species have often been referred to *Trochita* Schumacher, 1817 (type species *Turbo trochiformis* Born, 1778), but their shelves (Figures 62 and 65) spiral from an off-center position roughly a quarter of the diameter in from the aperture edge. A so-called pseudumbilicus at the upper end of the shelves in Figures 62 and 65 could result from reduction of an umbilicus such as that of *Garzasia*. The shelves of '*C.*' *diegoana* and '*C.*' *aperta* are narrower than shelves of *Garzasia* and expand across about one third of the aperture. They differ distinctly from that of *Trochita* (Figures 71–73), which has a sturdy spiraling internal shelf extending from the centered axis of coiling to the outer shell margin, giving the impression of dividing the circular aperture in half.

'*Calyptrea*' *diegoana* does not appear to be a direct descendent of *Garzasia*. Its similarity to '*C.*' *aperta* suggests an ancestor in the Old World Tethyan Sea and, like many of the other Early Cenozoic mollusks (Squires, 1987, 2003), it probably arrived onto the Pacific slope via a circum-equatorial current. These species '*C.*' *diegoana* and '*C.*' *aperta* do not have shelves similar to that of *Calyptrea chinensis* (Linnaeus, 1758), the type species of *Calyptrea*. In *C. chinensis*, the thin fragile shelf (Figure 68) occupies about a quarter of the apertural circle.

It arises from the apex with a folded-over edge that forms the umbilicus. At the open end of the umbilicus, the shelf edge abruptly veers counter to coiling direction and approaches the apertural margin at an acute angle. The total shelfal edge is sickle-shaped with a short handle (the umbilical edge) and a long curved blade (the outer margin of the shelf). This leaves a deep notch between the attachment of the shelf to the shell and a delicate, lobate shelf.

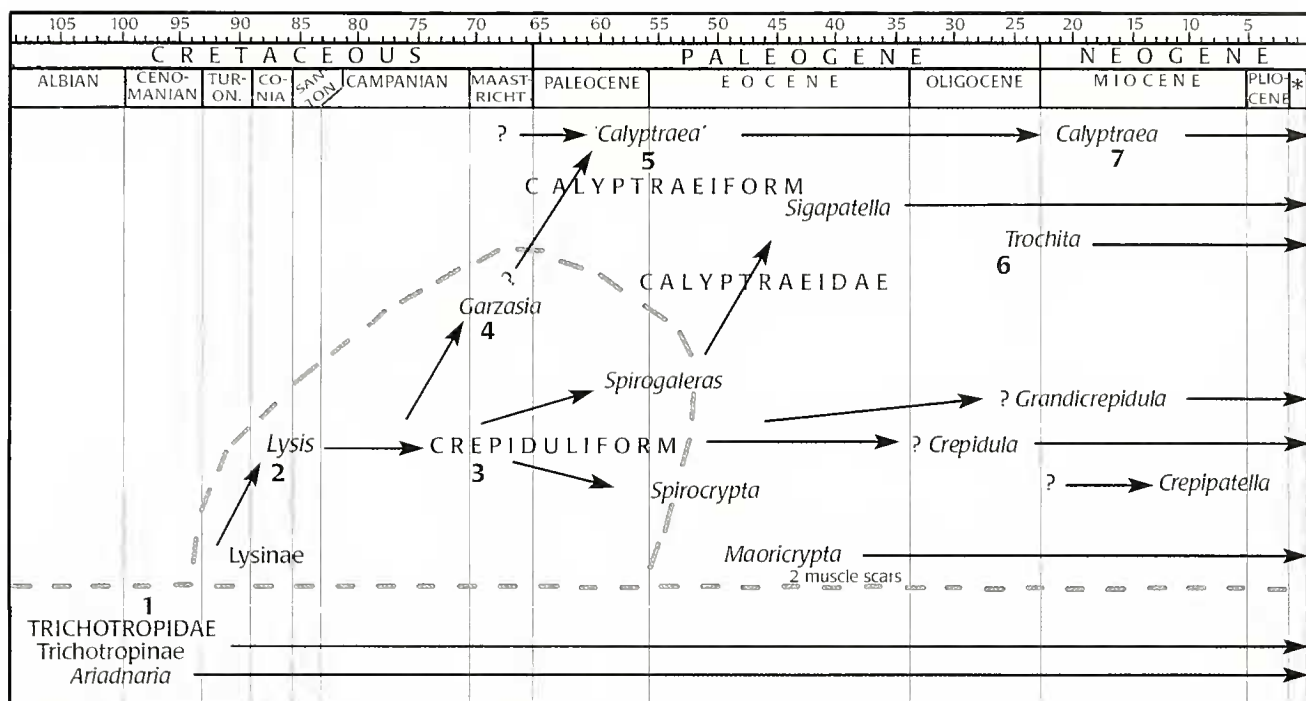
*Trochita* is present in modern eastern Pacific slope faunas from Mazatlan, Mexico to Valpariso, central Chile. It occurs in lower to middle Miocene strata as far north as the La Panza Range, San Luis Obispo Co., is present in the Kern River section, Kern Co. (Addicott, 1970) and the Topanga Formation, Santa Monica Mountains, Los Angeles Co., California. It has a thick shell with protractive ribbing and, as mentioned above, a sturdy shelf.

#### GLOBAL DISTRIBUTION OF CRETACEOUS LYSIFORM GASTROPODS

Both '*Crepidula*' and '*Calyptrea*' have been reported from Campanian and Maastrichtian age strata from throughout the world. Preservation of most specimens makes identification of them problematical. Some of these gastropods have proven to belong to other families or not to be of Cretaceous age. Others need verification. Our tally of occurrences is doubtless incomplete.

Although stated above as "throughout the world," these gastropods are recovered from areas that were probably temperate to tropical. Verified lysines are all younger than Turonian and older than Eocene. Classing *Spirogalacrus* as a lysine provides the only Paleocene record of this subfamily. Late Cretaceous occurrences suggest that the calyptraeids developed in several geographic places from widely distributed trichotropids evolving into Lysinae. An example of this is the evolving shape of *Lysis*. Although on the Pacific Slope calyptraeid-form calyptraeids developed from a crepiduliform calyptraeid, the calyptraeid form has been recognized more widely geographically, but not earlier than Coniacian.

Cretaceous calyptraeid-form calyptraeids are more widely recognized geographically than are crepiduliform calyptraeids. Europe has calyptraeid-form occurrences but no crepiduliform occurrences. Africa has calyptraeid-form occurrences in the north and crepiduliform occurrences in the south. African occurrences are close in time to those of the Pacific Slope. North America (exclusive of the Pacific Slope) has a very few reports along the Gulf Coast of calyptraeid-form specimens. The Pacific Slope has both calyptraeid-form *Garzasia* and crepiduliform *Lysis*. South America has calyptraeid-form species. Japan somewhat mirrors the Pacific Slope. Its known lysine is of early Maastrichtian age, but the additional presence of a trichotropid (Kase, 1990) similar to *A. obstricta* suggests that lysines were developing there roughly synchronously with those along the Pacific Slope. New Zealand has no



**Figure 74.** Generalized proposed evolutionary trends of calyptraeoids. Time scale after Gradstein et al., 2004. Calyptraeids and crepidulids probably evolved from several trichotropids. *Lysis* or *Lysis*-like fossils of Coniacian to Maastrichtian age have been described from California, and from Campanian to Maastrichtian age from southern Africa and Japan. **1.** Turriculate gastropods having gill capable of filter feeding, sedentary adult life on hard substrate. Probably capable of copulation, protandrium, and brooding of young. **2.** Broadening of columella and inner lip. Enlarging final whorl. **3.** Attachment of posterior shelf end to interior of outer lip to develop crescentic shelf. **4.** Some species developed "umbilicus" in spiraling shelf as in *Garzasia*. **5.** "Umbilicus" closed or nearly so in Eocene *Crepidula* and moving toward more central position in more circular base. **6.** Broad shelf, spiraling from near center of base. Shelf edge nearly straight. **7.** Spiral shell with low spire, round base. Shelf edge extremely sigmoidal. \* = Pleistocene. Stages abbreviated are Turonian, Coniacian, Santonian, Maastrichtian.

known Cretaceous lysines but does have the youngest known calyptraeiform lysine.

**EUROPE:** *Crepidula mytiloidea* Bellardi and Michelotti, 1840 from Villavernia near Tortona Italy was listed among Nomina Dubia by Hoagland (1977) as being from the Cretaceous. Bellardi and Michelotti were describing a Tertiary fauna. Because the specimen and illustrations are so small, Hoagland could not verify that this species was a *Crepidula*.

*Calyptreaa eretacea* (d'Orbigny, 1842: 390, pl. 234, figs. 1–3) [*Infundibulum*] was examined by Kollmann (2005) who determined that d'Orbigny's material was from Campanian of Charente-Maritime, southern France, and that the specimen identified as *C. eretacea* by Delpy (1942: 165, fig. 1) was from Maastrichtian of southwestern France. Poor preservation of d'Orbigny's type caused Kollmann (2005: 172, pl. 18, fig. 18) to refer to it as "*Calyptreaa s. lato eretacea* (d'Orbigny, 1843), *species dubia*." Delpy's illustration shows no shelf. Kollmann considered both specimens to be only *Calyptreaa* sensu lato. These specimens expand their whorl diameter much less rapidly and have much higher spires than specimens of *Lysis* and *Garzasia* from the Pacific Slope of North America.

*Calyptreaa depressa* Delpy, 1942 (p. 165, fig. 2) from

Maastrichtian southwestern France, has a spiraling shelf similar to that of Eocene *'Calyptreaa' aperta* except that its shelfal margin is concavely arcuate between rim and whorl center.

Kollmann and Odin (2001: 446, pl. 1, figs. 18–19) recorded *Calyptreaa* sp. of Maastrichtian age from southwestern France, but the preservation of the specimens appears to be too poor to allow positive generic identification.

**AFRICA:** As figured, *'Calyptreaa' bouéi* (Pervinquière, 1912: 10–11, pl. 1, figs. 7–11) from the Maastrichtian of Tunisia externally resembles some forms assigned to *'C.' aperta*. The shape of the shelf of *'C.' bouéi* shown in figure 9 is difficult to determine, but appears to have a straight edge and probably resembles that of *'C.' aperta*.

*Galerus libyca* Quaas, 1902, was described from upper Maastrichtian/possibly Danian strata (*Exogyra overwegi* beds) from the Ammonite Hills, Great Sand Sea, Egypt (Quaas, 1902: 238, pl. 25, figs. 26–29). It has been reported also from the Congo (Darteville and Brébion, 1956: 29–30, pl. 1, figs. 9–10), and from Libya, Egypt, Congo, and Madagascar (Bandel and Riedel, 1994: 339–340, pl. 7, figs. 2–3). Bandel and Riedel reported Quaas' original specimens lost in World War II and figured the

exterior of a subsequently collected specimen of *Calyptraea libyca* which resembles *C. aperta*. They did not figure the shelf, but described it too briefly as "a flat spiral shelf like that of modern *Calyptraea*."

A *Crepidula* chain was reported by Brébion (1956) in describing *Crepidula congolensis* Brébion, 1956, from the upper Campanian of the Congo, Africa. This African species resembles a *Lysis* more than it does a modern *Crepidula*, in that *C. congolensis* has coiling similar to *Lysis* and a depressed inner lip that barely wraps onto the labral side of the aperture. *Lysis? congolensis* (Brébion, 1956: 89, fig. 1; pl. 1, fig. 7a, 7b) is most similar to *L. jalamaca* in shape and sculpture but appears to have much finer ribbing than *L. jalamaca*.

*Calyptraea primogenita* Kiel and Bandel (2003: 460, fig. 4.14–4.16) and *Lysis capensis* (Rennie, 1930) illustrated by Kiel and Bandel (2003: 460, fig. 6.1–6.2) are from the upper Santonian/lower Campanian, Umzamba Formation. *Calyptraea primogenita* was described from a single worm and broken specimen. Its ribbing (except on last quarter-whorl) is protractive as in *Trochita*, and it has a thick shell as does *Trochita*. Its whorl shape is more trochiform than in *Trochita* or *Calyptraea*, it consists of more whorls than a *Trochita* or a *Calyptraea*, the last whorl lacks the notable enlargement of a *Trochita* or a *Calyptraea*, and unlike *Trochita* or *Calyptraea*, it has a small open umbilicus and "the columellar lip bears a strong plate" (Kiel and Bandel, 2003).

*Lysis capensis* is very similar in shape and sculpture to *L. duplicosta*, but its inner lip seems narrower and more similar to that of *L. mickeyi*. *Lysis duplicosta* is generally lower spired and has a broader inner lip/columella.

Rennie (1945: 50, 116, pl. 3, fig. 10) figured a *Calyptraea* sp. from the Upper Cretaceous Senonian of Angola, Africa. A more precise age is unknown and, although the shape and angle of suture in the figure resemble *Calyptraea*, the base and aperture are not illustrated, thereby making generic assignment indeterminate.

NORTH AMERICA (exclusive of the Pacific Slope): *Crucibulum?* sp. of Sohl (1960: pl. 10, fig. 21) is an immature, incomplete specimen from the upper part of the Ripley Formation (Maastrichtian) in Mississippi. Sohl indicated that its incomplete shell suggested a close relationship to *Crucibulum*, and that it definitely appeared to belong in the Calyptraoidea. The specimen is too incomplete to determine its genus, its similarity to *Crucibulum* could be a result of the way it is broken, but its spire does suggest Calyptraoidea.

Sohl (1960) classed *Thylacrus cretaceus* Conrad, 1860 in Capulidae, but Dockery (1993) moved it to Calyptraeidae and Bandel and Riedel (1994) included Conrad's species in Hipponicidae. It apparently lived attached to the columella within the aperture of empty gastropod shells. It differs from *Lysis* and *Garzasia* in the way *Thylacrus* muscles were attached. At the end of juvenile coiling and beginning of expansion of the last whorl, *Thylacrus* deposited left and right prongs instead

of modifying the inner lip/columella into a shelf as in *Lysis*. Sohl (1960: pl. 10, fig. 4) and (Dockery (1993: pl. 18, figs. 1 and 4) provided good illustrations of the early development which does seem more hipponicid than calyptraeid. When developed to maturity a horse-shoe-shaped muscle scar resulted. Dockery's (1993) specimens were from the Coffee Sand of Campanian age and Sohl's (1960) from the Ripley Formation of Maastrichtian age.

SOUTH AMERICA: *Calyptraea aperta* (Solander in Brander, 1766), a European Eocene species (see Figures 65–67 for a representative late Eocene specimen from the Paris Basin, France), was identified by Olsson (1944: 248–249, pl. 9, figs. 10–13) from northern Peru. Olsson's placement of the Tortuga fossil beds below his Radiolite sandstones with *Baculites* suggests a Maastrichtian age. As he provided only exterior views and no description of the shelf, this identification needs further verification. Specimens identified as *Calyptraea aperta* from Europe and the American Gulf Coast range widely as to whorl height and sculpture which varies from smooth to spinose. The Peruvian specimens increase in diameter at a slower rate and they have more strongly impressed sutures than Eocene specimens, suggesting that the Peruvian specimens are probably not *C. aperta*.

*Calyptraea laevis* (Philippi, 1857) from Maastrichtian of central Chile was described as *Trochita laevis* Philippi (1857: 92, pl. 11, fig. 3; referred to *Galeropsis* by Wilckens (1904: 195–196, pl. 17, figs. 9a, b) because of its high spire, and to *Calyptraea (Trochita)* by Bandel and Stinnesbeck (2000: 763–764, pl. 1, fig. C). Bandel and Stinnesbeck provided a view of the exterior only, and described the shelf as "a flat concave shell like that of modern *Calyptraea*." Although "flat concave shell" might partially describe a *Trochita* shelf, it is not an accurate description of the shelf in *Calyptraea chinensis* (Figure 68). Wilckens (1907: 13, pl. 3, fig. 6) also reported *Calyptraea* aff. *laevis* Philippi of Maastrichtian age from southern Patagonia, but the preservation of the specimen appears to be too poor to allow positive generic identification.

*Calyptraea pileolus* d'Orbigny, 1841 was indicated by Hoagland (1977: 354) to have been recorded from Lower Cretaceous strata of Argentina by von Ihering (1907), but the species was listed by Ferraglio (1937: 187) from the Patagoniano (Tertiary) of Lago Argentino, Argentina.

JAPAN: As noted earlier, *Lysis izumiensis* Kase, 1990 has been described from the earliest Maastrichtian of Japan. It resembles the group of *Lysis duplicosta* and appears from the illustrations (Kase, 1990: figs. 2.11–2.12) to be most similar to *L. duplicosta* in strength of sculpture and development of innerlip/columellar expansion. Kase (1990) also recorded a trichotropid similar to *Ariadnaria obstricta* from the Izumi Group in Japan.

NEW ZEALAND: The early Paleocene (Danian) *Spirogalaerus* Finlay and Marwick, 1937, from New Zealand is *Lysis*-like, especially as to growth line, and this similarity requires further study to determine whether it



results from common ancestry, convergent evolution, or parallel evolution. Finlay and Marwick (1937) assigned *Spirogalerus* to family Calyptraeidae and based their genus on *Spirogalerus lamellaria* Finlay and Marwick, 1937, which resembles *L. suciensis* except that *L. suciensis* lacks the "pseudumbilicus" described for *Spirogalerus*. Finlay and Marwick (1937) and Boshier (1960) opined that *Spirogalerus lamellaria* could represent the evolutionary link between erepidulids and calyptraeiform *Sigapatella* Lesson, 1830.

Classification of *Spirogalerus* has been inconsistent. Wenz (1940) made it a subgenus of *Calyptraea* Lamarck, 1799. Beu and Maxwell (1990) made *Spirogalerus* a subgenus of the calyptraeid *Sigapatella* Lesson, 1830, but Stilwell and Zinsmeister (1992) separated *Sigapatella* from *Spirogalerus* because the latter has a strongly exerted spire. Collin (2003a) noted that *Sigapatella* has a shell and anatomy similar to the calyptraeid genera *Calyptraea*, *Trochita* Schumacher, 1817, and *Zegalerus* Finlay, 1926. Collin (2003b) considered *Sigapatella* to be monophyletic but did not mention *Spirogalerus*. Marshall (2003) recognized *Sigapatella* (= *Zegalerus*) as a distinct genus based on its shelf edge being broadly and evenly concave instead of sigmoidal. This is a very different shelf than that of *Calyptraea chinensis* (Figure 6S). The differences between *Spirogalerus* and *Sigapatella* are similar to those found between *Lysis* and *Garzasia*, and the New Zealand forms also record an evolutionary pattern of enlargement of the last whorl and the aperture, with broadening of the columella/inner lip area into a shelf within a limpetiform shell. Thus, these two genera were probably not links from actual erepidulids, but represent links from lysines to calyptraeids.

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- ## APPENDIX 1
- ### LOCALITIES CITED
- Localities are LACMIP, unless otherwise noted. All quadrangle maps are U. S. Geological Survey maps. Bracketed numbers are areas shown on Figure 1.
- [4] CASG 61794. [= CAS 1346-A]. In conglomeratic sandstone 1.6 km (1 mi.) above mouth of Huling Creek, North Fork Cottonwood Creek, Ono Quadrangle (15 minute, 1952), Shasta Co., California. Budden Canyon Formation, Bald Hills Member. Late Albian.
7333. Le Fayel, Paris Basin, France. Late Eocene (Bartonian Stage).
- [15] 10095. [=CIT 53]. Fine sandstone just above shale, sectionline fence gate on old road 0.4 km (1/4 mi.) W of Schulz Ranch, 122 m (400 ft.) S. of northeast corner of section 19, T. 5 S. R. 7 W, El Toro Quadrangle (7.5 minute, 1965), south side of Williams Canyon, Santa Ana Mountains, Orange Co., California. Coll.: B. N. Moore, 1 January, 1926. Ladd Formation, uppermost Holz Shale Member. Early Campanian.
- [16] 10711. [=CIT 1155]. Approximately 1.84 km (1.5 mi.) due west of Los Angeles-Ventura Co. line on the boundary (extended) between T. 1 N and T. 2 N, north bank of Bell Canyon, southeast slope of Simi Hills, Calabasas Quadrangle (7.5 minute, 1952), Ventura Co., California. Coll.: W. P. Popenoe, 15 July, 1935. Chatsworth Formation. Middle Campanian.
- [3] 10757. [=CIT 1593]. Massive sandstones in bed of North Fork Bear Creek, approximately 777 m (2550 ft.) south and 533 m (1750 ft.) east of northeast corner of section 5, T. 31 N, R. 1 E, Whitmore Quadrangle (15 minute, 1956), Shasta County, California. Coll.: W. P. Popenoe and W. M. Tovell, 12 Sept., 1941. Redding Formation, Bear Creek Sandstone, Coniacian.
- [5] 10546. [=CIT 1014]. Concretions in sandstone, right bank of Chico Creek about 1.6 km (1 mi.) upstream from the little bridge across creek below Mickey house and about 4.16 km (2.5 mi.) N6°W of 14-mile house on Humboldt Road, NW 1/4, SE 1/4 of section 1, T. 23 N, R. 2 E, Paradise Quadrangle (15 minute, 1953), Butte Co., California. Coll.: W. P. Popenoe and D. W. Scharf, 16 August, 1931. Chico Formation, top of Ponderosa Way Member. Late Coniacian or early Santonian.
- [23] 11944. Approximately 10 km N of Punta Abreojos (SW of San Ignacio), in first ridges N of arroyo that crosses Punta Abreojos road (dirt) just S of Campo Rene turnoff, approx. 2 km NW of road. Approx. 2–3 km up ravine, hill .5 km to east is pachydiscid loc., Viscaiano Peninsula, Baja California Sur, Mexico. Coll.: R. Demetrios, 1987, 1989. Valle Formation. Middle? Campanian, with *Hoplitolpacenticeras*?
- [14] 14310. About 450m north and 70m west of lookout at summit of Warm Springs Mountain at elev. of 1052 m (3450 ft.), at base of Kirby's (1991, M. A. Thesis) measured section no. 2, Warm Springs Mountain Quadrangle (1958), Los Angeles County, California. Coll.: M. N. Kirby. Basal San Francisquito Formation. Late Maastrichtian.
22340. Gritty conglomeratic sandstone lenses in fine-grained sandstone and shales, east side Grapevine Canyon about 0.8 km (0.5 mi.) south of its north end, about 0.4 km (0.25 mi.) east of, and 30.48 m (100 ft.) above the abandoned highway roadbed on east side of canyon, at about 645 m (2100 ft.) contour, about 91 m (300 ft.) northwest of Tejon/granite fault contact. Locality is 3048 m (10,000 ft.) N24°W of 3174 ft. BenchMark at old Fort Tejon, Tejon Quadrangle, Kern County, California. Coll.: W. P. Popenoe, 9 December, 1946. Tejon Formation. Middle Eocene.
22386. Prominent shell bed at crest of ridge on east side of Live Oak Canyon, about 0.4 m (0.25 mi.) south of its mouth, T 10 N, R 19 W, Pastoria Creek Quadrangle, 7.5', 1955, photorevised 1974, Kern County, California. Coll.: W. P. Popenoe, 13 March, 1947. Tejon Formation, Metrala Sandstone Member. Middle to upper Eocene ("Tejon Stage").
- [10] 22585. About 2/3 of the way to the top of a gully on southwest slope of a northwest-trending hill on south side of Garzas Creek, where the creek enters the San Joaquin Plain, approximately 610 m south and 183 m west of northeast corner of section 19, T 8 S, R 8 E, Howard Ranch Quadrangle, 7.5', 1953, photorevised 1971, west side of San Joaquin Valley, Stanislaus Co., California. Coll.: W. P. Popenoe and T. Susuki, April, 1950. Moreno Formation, "Garzas Sand" member. Middle Maastrichtian.
- [4] 23464 [PR1] Up small creek from Sullivan Ranch Rd. crossing, and 1.28 km (0.8 mi.) north of ranch, near Gas Point Rd., 791 m (2300') N 75°E from mouth of Huling Creek, 579 m (1900') S, 485' (1600') E of NW corner of section 16, T. 30 N, R. 6 W, Ono Quadrangle (15 minute, 1952), Shasta Co., California. Coll.: P. U. Rodda and M. A. Murphy, May 1955. Budden Canyon Formation, Bald Hills Member, unit iv in Matsumoto, (1960). Middle Cenomanian, probably *Turrillites costatus* Zone.
- [5] 23617. Fossil in hard, blue-gray concretion in gray-weathering buff sandstone approximately 15.2 m (50 ft.) below highest conglomerate, approx. 0.5 km (0.5 mi.) upstream from Mickey house on west side of Chico Creek, 1.52 m (5 ft.) above stream, 716.25m (2350 ft.) north, 609.6 m (2000 ft.) west of southeast corner of section 1, T. 23 N, R. 2 E, Paradise Quadrangle (15 minute, 1953), Butte Co., California. Coll.: R. B. Saul, 14 August, 1955. Chico Formation, top of Ponderosa Way Member. Late Coniacian or early Santonian.
- [5] 23639. In concretions in massive, greenish-gray sandstone, east bank of Chico Creek, west of meadow with large flat-topped, lava block at north edge near road, 373.38 m (1225 ft.) south and 292.6 m (960 ft.) west of northeast corner of section 23, T. 23 N, R. 2 E, Paradise Quadrangle (15 minute, 1953), Butte County, northern California. Collectors: L. R. Saul and R. B. Saul, 20 August, 1952. Chico Formation, lowermost part of Ten Mile Member. Early Campanian.
- [12] 24122. Fine- to coarse grained buff sandstone; 76.2 m (250 ft.) north of jeep trail in Jalama Canyon; elevation 190 m (625 ft.), 6.58 km (4.11 mi.) east and 1.1 km (0.69 mi.) south of Jalama Ranch Headquarters; 0.93 km (0.58 mi.) west and 0.66 km (0.41 mi.) north of southeast corner of topo, Lompoc Hills Quadrangle (7.5 minute, 1959), Santa Barbara Co., California. Coll.: D. Dailey, August, 1959. Jalama Formation. Late Campanian–early Maastrichtian.
- [12] 24128. Dark gray conglomerate in first small canyon east of Ramajal Canyon, elevation 167.6 m (550 ft.), 0.54 km (0.34 mi.) south, 3.25 km (2.03 mi.) east of Jalama Ranch Headquarters, 1.22 km (0.76 mi.) north 4.27 km (2.67 mi.) west of southeast corner of Lompoc Hills Quadrangle (7.5 minute, 1959), Santa Barbara Co., California. Coll.: D.

Dailey, August 1958. Jalama Formation. Late Campanian–early Maastrichtian.

[12] 24237. Medium-grained, buff, arkosic sandstone, 396.2 m (1300 ft.) north of Jalama Creek, elevation 160 m (525 ft.), 0.48 km (0.30 mi.) south, 3 km (1.88 mi.) east of the Jalama Ranch Headquarters, 1.28 km (0.80 mi.) north, 4.59 km (2.87 mi.) west of southeast corner of Lompoc Hills Quadrangle (7.5 minute, 1959), Santa Barbara Co., California. Coll.: W. P. Popenoe, September 1938. Jalama Formation. Late Campanian–early Maastrichtian.

[6] 24340. Penz vicinity, conglomerate beds cropping out just below a drainage canal, southeast side of new Oroville Hwy, about 1.2 km (0.75 mi.) northeast of intersection with Pentz-Magalia-Oroville road, 426.7 m (1400') S., 182.9 m (600') W of the northeast corner of section 36, T. 21 N, R. 3 E, Cherokee quad. (7.5 minute, 1949), Butte Co., California. Coll.: W. P. Popenoe, 1960. Chico Formation, Musty Buck Member. Early Campanian.

[8] 24349. [=USGS M8601 and USGS M8745]. In place? large angular block of sandstone surrounded by sand at shoreline in covelet on north side of elongate seaward-pointing rock; approx. N30°W of Pigeon Point lighthouse, just south of Bolsa Point, Pigeon Point Quadrangle (7.5 minute, 1952), San Mateo County, California. Coll.: L. R. and R. B. Saul, October 11, 1960. Pigeon Point Fm. Middle Campanian.

[16] 26020. [=CIT 1158]. Hard sandstone slabs in fine-grained sandstone, cropping out on high bare cliff, north bank of Bell Canyon, just east of mouth of large gully, and 152.4 m (500') S, 2743.3 (9000') west of northeast corner of section 4, T. 1 N, R. 17 W, Calabazas Quadrangle (7.5 minute, 1952), Simi Hills, Ventura Co., California. Coll.: W. P. Popenoe, 11 Feb., 1972. Chatsworth Formation. Middle Campanian.

[10] 26353. Approximately 1.2 km south of Garzas Creek, 671 m south and 114 m east of northwest corner of section 20, T. 8 S, R. 8 E, Howard Ranch Quadrangle, 7.5', 1953, photorevised 1971, Stanislaus County, California. Coll.: R. B. Stewart and W. P. Popenoe, 1944. Moreno Formation, "Garzas Sand" member. Late early to early late Maastrichtian.

[11] 26370. Reworked fossiliferous Turonian blocks in upper Campanian conglomerate lens in shale, northeast side of Cooper Canyon, approx. 411.5 m (1350') N, 670.6 m (2200') W of southeast corner of section 2, T. 21 S, R. 14 E, Alcalde Hills Quadrangle (7.5 minute, 1969), Alcalde Hills, Fresno Co., California. Coll.: J. Alderson, 18 June,

1977. Panoche Formation, "Alcalde Shale" Member. Late Turonian (with juvenile *Subprionocyclus* sp.).

[18] 26951. Small sandstone lens approx. 6.1 m (20 ft.) above road in roadcut on north side of Silverado Truck Trail, 274.3 m (900 ft.) south of northeast corner of section 18, T. 5 S, R. 7 W, El Toro Quadrangle (7.5 minute, 1949), Orange Co., California. Coll.: A. A. Ahlgren, 4 Dec., 1981. Ladd Formation, uppermost Upper Holz Shale Member. Late early Campanian.

[17] 26967. Small exposure of coarse-grained, poorly sorted sandstone at bottom of northwest-flowing tributary to main fork of Garapito Creek, 449.6 m (1475 ft.) and 2835 m (9350 ft.) east of northwest corner of section 5, T. 1 S, R. 16 W, Topanga Quadrangle (7.5 minute, 1952, photorevised, 1981), Santa Monica Mountains, Los Angeles County, California. Coll.: J. M. Alderson, 31 Dec., 1981. Tuna Canyon Formation. Coniacian.

[3] 28717. South Cow Creek Valley, sandstone associated with conglomerate, lower South Cow Creek Valley, about 152.4 m (500 ft.) downstream from old bridge site across creek, and about 1.6 km (1 mi.) due west of buildings on Hunt Ranch, NE 1/4 of section 17, T. 31N, R. 2W, Millville Quadrangle, Shasta Co., California. Coll.: W. P. Popenoe, 27 Oct., 1971. Redding Formation, Oak Run Conglomerate Member of Haggart, 1986. Late Santonian.

[19] SDNHM 3403. Taylor Made Golf Facility at Salk Drive and College Blvd., elevation 45.1 m (148 ft.) along College Blvd., lat. 33°8'25' N, long. 117°16'56' W, [in general = SDNHM 3402, 3404, 4071, 4073], Carlsbad Research Center, Site 29, San Luis Rey Quadrangle 7.5' (1968), San Diego Co., California. Coll.: B. O. Riney, 26 April, 1987. Point Loma Formation. Late Campanian/early Maastrichtian.

[19] SDNHM 3405. Carlsbad Research Center, 1.6 km north and 2.7 km west of southeast corner of San Luis Rey Quadrangle 7.5' (1968), indicated area along west side of College Blvd. starting about 0.32 km from intersection with El Camino Real extends southward for 0.15 km, San Diego Co., California. Coll.: B. O. Riney, 1987. Point Loma Formation. ?Late Campanian/early Maastrichtian.

[18] UCMP 2167. 3.2 km (2 mi.) N 10°W of BM 1271, Corona Quadrangle (1902), at a gate about 0.8 km (0.5 mi.) below Modjeska Springs in Williams Canyon, Santa Ana Mountains, Orange Co., California. Ladd Formation, uppermost Holz Shale. Middle? Campanian.